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PROCEEDINGS OF

THE LINNEAN SOCIETY OF LONDON

162nd Session (1949–50)

Vol. 162 **Part 2**

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PROCEEDINGS OF

THE LINNEAN SOCIETY OF LONDON

Session 1949–50.

Vol. 162 Part 2

PROCEEDINGS OF THE GENERAL MEETING ON 9 March 1950

Professor F. E. Fritsch, F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on Thursday, 23 February 1950, having been circulated, were taken as read and confirmed.

The following message conveying congratulations to Dr. Reinhard Dohrn, F.M.L.S., on the attainment of his 70th birthday anniversary and on the completion of fifty years' association with the Marine Biological Station, Naples, was approved with acclamation.

To Dr. Reinhard Dohrn, F.M.L.S.

The President, Council, Fellows and Associates of The Linnean Society of London, being assembled together at their Meeting on the 9th March 1950, do hereby send to Dr. Reinhard Dohrn, Director of the Marine Biological Station, Naples, Italy, and a Foreign Member of this Society, their cordial greetings. They offer him their very hearty congratulations and good wishes on the attainment of his 70th Birthday Anniversary and on the completion of an association of fifty years with the Marine Biological Station. They recall with pride that Dr. Reinhard Dohrn has been a Foreign Member of the Linnean Society since 1937. They hope that for many years to come he will live to be the Companion, Guide and Friend of all those who may be privileged to work at the Laboratory.

To every Student of Marine Biology the name of Dohrn (father and son) will always be associated with that of the Marine Biological Station at Naples and linked with the invaluable contributions to our knowledge of Marine Organisms which have appeared in its publications. Students all the world over owe a great debt of gratitude to Dr. Dohrn and his father for their successful efforts to maintain the existence and integrity of the Naples Laboratory through two world wars.

9 March 1950.

F. E. Fritsch, *President.*
F. C. Stern, *Treasurer.*
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A. Tindell Hopwood, }

[A reply from Dr. Dohrn is printed on p. 191.]

The following were thanked for gifts made to the Library since the last Meeting :—The Hon. W. J. L. Palmer, Major Albert Pam, O.B.E., Mr. H. V. Rose, Dr. W. Watson and Professor F. E. Weiss, F.R.S.

The following Fellows signed the Obligation in the Roll and Charter Book and were admitted Fellows :—Miss Eleanor Mary Ord Laurie and Dr. Hamish Boyd Gilliland.

Certificates of recommendation for election to Fellowship of the Candidates named in the Agenda of the present General Meeting were taken as read for the first time.

The President reported the death of Professor René Maire, Foreign Member.

A DISCUSSION ON TIME-RATES IN EVOLUTION was opened by Prof. F. E. ZEUNER and Prof. JAMES SMALL.

In the general discussion the following took part :—The President, Mr. F. J. Manning, Mr. R. Ross ; Prof. Zeuner and Prof. Small replied. [Printed below.]

The following papers were read in title,—

'A new method for the identification and study of critical groups'. By the late A. J. WILMOTT, M.A., F.L.S. [Printed in Proc. Linn. Soc. *162*. Part 1.]

'Notes on Charophytes from British Columbia'. By G. O. ALLEN, M.A., F.L.S. [Printed below, p. 148].

A DISCUSSION OF TIME-RATES IN EVOLUTION

TIME-RATES IN ORGANIC EVOLUTION

By F. E. ZEUNER.

The opening remarks in this discussion on Time Rates in Evolution are intended to summarize briefly the work done by a number of authors and thus to provide a general background. Since time-rates can only be obtained by comparing morphological changes observed in ancestral lines of fossils with an absolute geological time-scale, I have been asked to begin my contribution with a brief outline of the relevant time-scales.

A. TIME-SCALES.

The last thirty years have witnessed a great development of absolute time-scales in geology, and their application to palaeontology has opened a new field for work on the time-rates of organic evolution. In this it is necessary to be aware both of the degree of reliability and of the limitations of the time-scales used. Three kinds of scales are important for studies in organic evolution, namely those based on (*a*) radioactivity, (*b*) Pleistocene climatic oscillations, and (*c*) varve counts.

Radioactivity scales.

Several time-scales have been based on phenomena of radioactivity. The most important one relies on the disintegration of uranium, which produces lead and helium in the course of time. The quantities of disintegration products accumulated near an uranium mineral give the clue to its age. Our knowledge of the duration of geological periods prior to the Pleistocene is largely based on this method. It has been refined by a close comparison of results with those obtained from relative thicknesses of sediments formed in the sea in successive periods. This comparison, made by Holmes, places the beginning of the Tertiary at 60–70 million, of the Triassic at 180–200 million, of the Carboniferous at 255–275 million, of the Silurian at 350 million and of the Cambrian at 510 million years ago.

The values obtained by the uranium–lead method have been greatly improved by isotopic analysis of the lead. There are some other methods based on radio-activity of minerals, such as the investigation of pleochroic halos and of the

radioactive transformation of rubidium into strontium, but these are for the time being of a subsidiary character.

Two other methods based on radioactivity offer to provide dates for parts of the Pleistocene and the Postglacial. One is based on the investigation of long cores of deep-sea sediments. In these radium is found in quantities which are much too large to be accounted for by its normal development as a member of the disintegration series of uranium. It is assumed, therefore, that radium is precipitated chemically in ocean sediments. The decomposition of this radium provides a dating method for layers of deep-sea sediment up to about 300,000 years old, but its applicability is much reduced by a number of unsolved problems, such as the precipitation of radioactive elements from sea-water, the rate of sedimentation, and the diffusion of radium in sediments. Only a few results have been obtained, which suggest that the duration of the Pleistocene is of the order of several hundred thousand years. Another radioactivity method has been developed quite recently by W. F. Libby, which relies on the disintegration of radioactive carbon (C^{14}) in dead organic matter and covers a period of about 20–30,000 years. A large number of determinations have already been made, which suggest that our conceptions of the duration of the Postglacial, based on varve methods and astronomical estimates, are correct.

Time-scales for the Pleistocene.

For studies in the time-rates of speciation, the Pleistocene period provides a large proportion of the evidence. Radioactivity scales have only supplied a very vague estimate of the order of 1 million years for the duration of the Pleistocene. Dating, therefore, relies mainly on the combination of stratigraphical research (which has developed a sequence of sub-divisions based on climatic oscillations) with a number of 'time-gauges' derived from the rates of weathering, denudation, sedimentation and astronomical cycles. Considering the difficulties involved, the results must be regarded as reasonably consistent.

Four large glaciations, divided into minor phases and three large interglacials have been recognized, both in Europe and North America, and accepted as the basis of Pleistocene stratigraphy. By using the rate of weathering and of deposition of annual sediment in certain Swiss Lakes, Penck determined the duration of time which has elasped since the Last Glaciation as of the order of 15–20,000 years. Using this as a time unit and comparing the effects of weathering, denudation and sedimentation in the three interglacials, he obtained estimates for the duration of the Pleistocene since the beginning of the First Glaciation. The result was 600,000 years. In America, Kay used weathering phenomena for the same purpose, but he had to extrapolate from the poorly-founded estimate of 25,000 years since the beginning of the retreat of the last ice-sheet. He obtained 675,000 years for the duration of the interglacials and the time since the maximum of the Last Glaciation. To this has to be added the purely conjectural duration of the glaciations themselves, making a total of 700,000 to well over 1 million years according to the views of the estimators. Since the radio-carbon method has recently provided dates for the 'Postglacial' which appear to reduce Kay's figure to about a half, the Pleistocene time-scale of this author is likely to fall into line with Penck's estimate.

Assuming that glacial phases were phases of cool summers with reduced melting combined initially with mild winters with increased precipitation, the slight variation of radiation received from the sun, and due to regular perturbations of the orbit by other planets, has been regarded as a possible cause, not of the Ice Age as a whole, but of its glacial and interglacial phases. On this method, which must not be confused with Croll's well-known but futile attempt to explain the Ice Age with the aid of one astronomical element distorting the orbit, is based the elaborate dating system designed by the astro-physicist, Milankovitch, and the climatologist, Köppen. The duration of the Pleistocene on this scale is again

of the order of 600,000 years. The results of the different methods of dating the Pleistocene are summarized in the following table:

	Proportion of Post-Glacial	to	Last Interglacial	to	Penultimate Interglacial	to	Ante-Penultimate Interglacial	Total Duration since Beginning of Günz
Penck	1	:	3	:	12	:	4	600,000 yrs.
Kay	1	:	5	:	12	:	8	700,000–1·2 million years.
Astronomical	1	:	3	:	8	:	3	600,000 yrs.

No matter, therefore, which time-scale is used, the order of magnitude of the period is known.

Varve method.

The method of counting annual layers of sediment, laid down mainly by melt-water of ice in Scandinavia and Switzerland, has been used extensively for the construction of a time-scale covering the period since the climax of the Last Glaciation. In spite of disagreement in detail, the results agree in the order of magnitude. In Switzerland Heim obtained 16,000 years, Steck 20,000–15,000 years. De Geer in Scandinavia made a total estimate of 18,000 years. There are other estimates covering portions only of the interval in question, such as the remarkable scale developed by Welten in Switzerland for the Postglacial forest history. The astronomical theory assigned about 20,000 years to the same period, which value agrees satisfactorily with those based on varve counts.

B. Number of Species and Higher Systematic Units Present in Subsequent Periods of Time.

The time-scales outlined have been used in statistical investigations of the number of species existing in successive periods, of genera or families, or of genera in families or orders and so forth. Information is thus obtained as to the number of new species produced by groups per unit of time and also the survival rates of species. The numerical material has been presented in various ways. Small, for instance, has used tables, rosette diagrams and other devices, whilst other workers like Simpson and Zeuner have preferred to sacrifice numerical completeness for the sake of simplicity and clarity by plotting the number of systematic units and the amount of change against the time on ordinary co-ordinates. Two aspects of time-rate problems can be studied in this way.

(*a*) The number of species *existing* in successive stratigraphical divisions is plotted. If the rate of speciation equals the rate of species extinction, the number of existing species will remain steady. But if the speciation rate is greater, then the number of species rises, more or less rapidly, along an exponential curve. Such curves can usually be divided into an initial lag phase, a more or less ' explosive ' increase phase, a stability phase, and one or more decline phases. The material suggests that the increase phase, if distinct, is of the order of 50–60 $\pm$30 million years, irrespective of the systematic categories investigated. It appears correct, therefore, to say that it takes no longer for a new order to evolve than for a new genus to appear.

It is, however, necessary to stress that this statistical picture of the evolution of a group is not always met with, though some workers tend to convey the impression that an ' explosive ' increase phase occurs, or has occurred, in every group. But there are many in which the increase has always remained very moderate, for instance in the Dipnoi.

(*b*) Alternatively the newly appearing species only may be plotted. In this way the survivors are eliminated. This procedure is applicable only in groups for which abundant material is available. From the comparison of the changes in number of the newly appearing species with that of the survivors, both Simpson (in Bivalve Mollusca) and Small (in Diatoms and Foraminifera) have deduced the presence of two different types of species survival. There appear to be species with short and with long life-times, the two types being clearly distinct and not linked by intermediates.

An interesting problem arises from this treatment of the material. If the increase phases are, broadly speaking, of the same chronological magnitude in both low and high systematic categories, is the number of steps involved in achieving the changes greater in the case of the higher systematic units than in the lower, or are the steps different in *quality*? This question has been raised by a number of workers in the field (e.g. Schindewolf, Simpson and Zeuner) and, indeed, in other fields such as genetics (e.g. Goldschmidt). The tendency has been to regard qualitative differences as significant. Simpson distinguishes them by the term *megaevolution*, Schindewolf *typogenesis*, Zeuner *aromorphosis*, whilst Goldschmidt introduces the term *macroevolution*. These terms, however, are not synonymous, though they all apply to the same phenomenon.

Moreover, a typogenetic phase, being characterized by a qualitative change, is not the same as the explosive phase mentioned previously during which evolution proceeds at maximum rates. On this point I am inclined to disagree with Professor Schindewolf's views. Very often, however, aromorphosis (or typogenesis) is followed by an ' explosive ' phase of increase in numbers, probably because the group has obtained a decisive advantage over the environment as the result of an advantageous mutation of the aromorph kind.

It may be objected that in studies of this kind the definition of the species concept is liable to impede comparison. It is true that attention has been drawn to this difficulty and that the taxonomic views of the specialists on whose work the statistical analyses rely, have to be taken into consideration. Within one and the same group, however, it is usually possible to achieve a high degree of consistency, so that numerical comparison becomes possible within such groups. It would, however, not be permissible to compare numerically with each other, without a very careful taxonomic investigation, groups in which the current species-definition is different, such as the Echinodermata, Mammals, Palaeozoic Cephalopods and Diatoms. The shapes of the curves are, of course, independent of the size of the unit. This is why the comparison of simple co-ordinate diagrams is to be preferred to the direct comparison of numbers.

C. The Tracing of Lineages in Time.

In groups where palaeontological evidence is sufficient to establish direct lines of ancestry (and the number of such groups is by no means small) it is possible to approach the problem of how much time is required for a new species to evolve from its immediate ancestor. Similarly, the period of existence of genera can be investigated from this angle.

There are undoubtedly cases of almost sudden appearance of new species, or groups of species, strongly suggestive of simple genetic mutation. Such cases are not frequent, however. Small's Diatoms appear, at least in part, to belong to this category, and also Schindewolf's Devonian Goniatites.

In other groups gradual evolution by means of steps very much smaller than a full species step is the rule. It is the usual condition in the animal kingdom, and particularly well illustrated by the lineage of the horse. If one plots the amounts of structural modification, either in the leg bones or the teeth, or some other morphological change, against the absolute geological time-scale, one observes, for instance, that the evolution from *Epihippus* to *Mesohippus* was a

great morphological step, though on the time-scale it took no longer than the small morphological step from *Orohippus* to *Epihippus*. Arbitrary steps have been used by workers in this field. Realizing the advisability of designing some quantitative measure for rates of evolution, Haldane has suggested the introduction of the *millidarwin*.

The horse lineage has made it evident that (*a*) the rate of morphological change is not a simple function of time and (*b*) at any point of the lineage there is not enough individual difference in the height of the cheek-teeth, nor even in successive species of ages as much apart as one million years, to believe that minute differences present had any value as determining factors in survival. This was deduced by Stirton from the evolution of hypsodonty in horse molars. Finally, the horse lineage suggests that (*c*) the average period of existence of a horse genus is about five and a half million years (Simpson). Other ' life-times ' of genera are:—carnivores (mean) six and a half million years, Triassic ammonites (mean) twenty million years, *Apis* thirty-five million years, Bivalves (mean) seventy-eight million years, *Lingula* four hundred million years. Genera of terrestrial mammalia thus appear to be relatively short-lived.

The question of how much time is required for the changes in a lineage to have accumulated to such an extent that taxonomists regard the product as a *new* species, can be attacked by the study of the Pleistocene material. For the sake of simplicity, the term species-step is used in this connection.

During the Postglacial, only some subspecies of a very inferior taxonomic value appear to have evolved in animals. Because of some striking external character, such as colour, length of hair, etc., they have often been described as species, though it is unlikely that they are genetically significantly distinct from their ancestors. The British Red Deer, for instance, regarded as a subspecies, has developed from one closely resembling the Continental race during the last 10,000 years. Its characters, however, are mainly due to degeneration, and specimens transferred to the favourable environment of New Zealand re-developed their ancestral characters within a few generations. Similar subspecies are found among insects.

Material from the Upper Pleistocene (about 50–100,000 years old) suggests that in some, but not all, mammalia the differences are of subspecific rank, though much more pronounced than in the examples from the Postglacial. Wehrli, for instance, found that in the Upper Pleistocene marmots the temporal ridges run into the upper posterior edge of the processus postorbitalis in many of the specimens, whilst in the recent type the temporal ridges have moved to the upper side of the process itself. This modern type is observed in 98 per cent of Recent specimens but only 37 per cent of Upper Pleistocene ones. This structural character, therefore, unstable in the Upper Pleistocene, has become almost constant in the Recent descendants.

In the Middle Pleistocene (about 250 thousand years ago) subspecific characters are the rule in many mammals, though specialist palaeontologists have often applied specific names to them. The differences observed do not, however, exceed those present in well-defined geographical subspecies of the Recent fauna. In the Lower Pleistocene (about half a million years ago) the differences compared with modern or Upper Pleistocene descendants are not infrequently large enough for the descendants to be regarded as a good new species. This applies, for instance, to elephants, bears and rhinoceroses. Of the mammalian fauna of the Lower Pleistocene Cromer Forest Bed only 14 per cent are regarded as belonging to Recent species. This figure would probably be somewhat larger if it were possible to study in the fossils all those characters which are used in the taxonomy of their surviving relations.

It appears that 500,000 years is a fast rate for a species-step. It would be a mistake to regard this as a maximum, though faster rates are evidently very exceptional in terrestrial mammals, insects and mollusca. A shorter rate, of

about 150,000 years has recently been claimed for Somaliland snakes by Parker. There is no reason why such exceptionally fast rate should not occur, though this rate was calculated on the basis of palaeoclimatic correlations which would equally lend themselves to longer alternative values.

On the other hand, slow rates for species-steps are observed in some groups, mainly marine. Lower Miocene species, for instance, have remained unchanged for 30 million years and even slower rates are quite conceivable especially among stable species, the existence of which Small has been stressing.

Among land forms, insects are of interest. Specific differentiation was in all probability rapid, and subspecific differences comparable with those found in mammals were observed in the Upper Pleistocene insect fauna of Starunia by Zeuner. But few major classes and not many genera arose after the Lower Tertiary. The genus *Drosophila*, for instance, has existed for at least 50 million years in spite of its great genetic pliability, without succeeding in trespassing beyond the bounds of its generic definition. If one recalls in this connection the fast rate of change in elephants and horses, it appears that there is no correlation between fast rates of species evolution and groups having rapid succession of generations. This was first observed by Zeuner in 1931 and independently again by Simpson in 1944. A rapid succession of generations, therefore, must not be taken as a substitute for long periods of time, as has been the prevalent practice in certain types of research in genetics.

Finally, it is worth mentioning the honey bee (*Apis mellifera L.*) as a case of slow evolution in which phylogenetic splitting appears to have been reduced to almost zero, and which promises to provide instructive information, since there is not only fossil evidence available, but the cytology of the group has been studied in detail by Manning. The fossil evidence suggests that considerable morphological changes took place from Eocene to Oligocene times in a period of perhaps not more than 10 million years. The Eocene ancestors (*Electrapis*) were in many respects like bumble bees. But the Oligocene bees were already essentially equipped like honey bees and very close to the modern *Apis mellifera*. Since that time 30 million years have elapsed with hardly any morphological evolution. That the Oligocene bee was already a social insect is probable, since the structure of the legs, tongue and abdomen are like those in modern worker bees. The Eocene bee, however, can hardly have had a social life higher than that of the bumble bees.

The relationship of *Apis* to *Trigona* and *Melipona*, bumbles, *Xylocopa*, etc., has been studied morphologically, and there is fossil evidence in Eocene times for the existence of several stocks of primitive Apids. *Trigona* and *Melipona* appear to have separated from the *Apis* stock about the end of the Eocene. Since cytological evidence obtained from both these groups suggests that polyploidy occurred in *Apis* after this separation, it is conceivable that the Oligocene bees were the first products of it. It is a curious fact that from that time onward the morphological change in the direct lineage of *Apis mellifera* has been virtually nil. In contrast, *Melipona* and *Trigona* have evolved dozens of species just as have done the numerous genera of the solitary bees. The evidence has suggested that the ability to produce numerous closely related species was lost in *Apis* at the same time when polyploidy was established and when the social system was developed to something near the present level. It is hoped that further work will enable one to see whether there is any causal connection hidden behind this chronological coincidence.

D. Conclusion.

In conclusion it may be added that the study of time-rates of evolution will provide an important background for the study of the ancestral line of Man. More important fossil hominids have been found in the last decade than in any preceding one, and it is to be hoped that in the not too distant future it will be

possible to apply some chronological method to the investigation of the Hominoidea. The way in which it may become possible to tackle this problem has been indicated by Haldane in his paper on Quantitative Measurement of Evolution Rates.

The chronological treatment of evolution which is the subject of to-day's discussion will undoubtedly promote what one might call a historical approach to the problem of life. Such approach is the natural one for the palaeontologist, for he has been trained in geological methods, but it is but rarely encountered among biologists, who thus are apt to overlook the large amount of valuable evidence relating to evolution which palaeontology has made available. On the other hand, in order to interpret the fossils, the palæontologist needs the enormous amount of knowledge of living flora and fauna which the biological sciences have accumulated. Let us hope that this new approach will lead to closer co-operation.

It might also be pointed out that the methods employed in the study of morphological changes in organisms in the course of time can, *mutatis mutandis*, be applied to other problems, as, for instance, that of the technological evolution of prehistoric man. The number and complexity of tool types used by primitive man in the Lower, Middle and Upper Pleistocene and in the sub-divisions of the Postglacial display the same features of a lag phase followed by a logarithmic increase phase as do evolving groups of organisms. I am far from seeing in this a connection of a mystical kind; it is merely the expression of the applicability of very simple mathematical laws to cases in which certain quantities increase at certain rates. But as a technique the methods outlined in this introduction may perhaps be usefully applied in some other fields also.

Summing up, it appears there are two important problems emerging from the work so far done on time-rates of organic evolution, namely (1) that whilst rates of production of new systematic units vary, phases of abundant production have been found to be limited in duration to a few tens of million years. What are the causes of this?

(2) The rate of change in ancestral lineages (the rate of speciation) varies, but it is rarely less than a few hundred thousand years. Is one justified in generalizing this inference?

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DISCUSSION ON TIME-RATES IN EVOLUTION

By James Small.

Since the history of diatoms includes records of about 770 species which have continued specifically unchanged from their various times of origin for millions of years up to the present time, and have thus in themselves shown no evolutionary

change, it becomes necessary to define the *kind of evolution* for which *time-rates* can be measured in diatom history.

The general factual picture of evolution is now one of progressive evolution by apparently large steps for the phyla, combined with diversification of genetic patterns *downwards* from phyla to families, genera, species and lower categories. The geological history of diatom families and genera has been of this kind, each family and each genus having started as one species. The allogamous pennate group has diversified from three to about 3600 species in about 70 million years.

It has been suggested that the absence of early records for any but a few pennate diatoms is due to a lack of freshwater deposits, but 37 out of 48 fossil pennate genera are marine, and it is also highly improbable that there is a correlation of ignorance and of numbers of species graded as is actually found.

In connection with this general picture it may be of interest to note that Sewall Wright says in his contribution to the recent book on *Genetics, Paleontology and Evolution*—' The multiplication of species relatively rarely leads to generic differences and still more rarely to families and higher categories by a gradual cumulative process. There seems to be a large measure of truth in the contention of Willis and Goldschmidt, that evolution works down from the higher categories to the lower rather than the reverse '. And earlier in the same survey of ' the evolutionary process ' he writes—' Subspecies on this view are only rarely incipient species '. Sewall Wright also includes *four* types of non-recurrent changes among the nine methods he gives for immediate change of gene frequency.

There is very little evidence in diatom history of any *gradual* change from one species to another or from one genus or family to another genus or family. The evidence available practically all favours the view that species and higher categories have arisen in the diatoms mainly by one-step mutations, a process which has been favoured by the dominance of uniparental multiplication. This dominance has been complete as far as is known in the centric diatoms, and has been only slightly modified by occasional biparental auxospore production in the allogamous pennate diatoms (not including the Fragilariaceae).

Under these conditions ' evolution ' must be taken to mean the historical development *in time* of genera and higher categories. In the diatoms there is little evidence of evolution within species, although a few of the fossil species of freshwater or brackish water deposits have developed some varieties, both temporary ecotypes and more permanent biotypes. The evolution which has occurred has consisted mainly in the appearance of new species and new genera and a few families, together with the extinction of some species and some genera. Extinction played a relatively minor part in the development of the allogamous Pennales ; only five genera are extinct in that group and they were all short-lived. Among the species of that group about 7/16ths of the new species arising in any one sub-period became extinct within their sub-period of origin: the other 9/16ths nearly all continued into Recent. No genus of the allogamous Pennales is known from pre-Tertiary time, and this group shows many of the characteristics of the first stages in group histories, such as relatively rapid expansion with the origins of some new genera and origins of still more new species, with very few extinctions either of genera or of such species as continued beyond their sub-period of origin.

The Centrales (centric diatoms) include a large proportion of genera which are known from Upper Cretaceous. Some of these genera extended into Neogene but are now extinct: most of them are even now still living, like many Cretaceous genera of flowering plants. Like the latter, these genera have included many species now extinct, and according to the records about three quarters, or 12/16ths, of the species did not continue beyond their sub-period of origin. These species, like 7/16ths of allogamous Pennales species, were of *short* duration, as contrasted with the other species which continued in existence for millions of

years and even up to Recent in hundreds of cases. In addition to the larger proportion (12 instead of 7 sixteenths) of short-lived species, there is here a proportion of extinct or senescent genera, dead or represented by only a few long-lived species, and also a larger proportion of extinct species which have had durations extending into three or more sub-periods. Each of the ten sub-periods used as a time-scale is approximately one-tenth of 70 million-years, so a long-lived species has continued specifically unchanged for at least more than 7 m.y.

The time-rates of this 'evolution' cannot be measured by continuous morphological changes as has been done for horse lineages, but the intervals between successive one-step non-recurrent specific or generic mutations can be read from a tabulated summary of the history of each genus, if the duration of each species is indicated by a line drawn parallel to the time axis or by a dot for short-lived non-parental species. These short-lived species cannot be regarded as possible parents for any species which began in subsequent sub-periods: they were not in living existence then. The abrupt beginnings of species-histories involve contemporaneous existence of parent and progeny.

My numerical analyses of the known history of the numbers and durations of species and genera of diatoms has been based upon this time-scale of what I call 'sub-periods'. The epochs of the Tertiary period, Paleocene, Eocene, Oligocene, Miocene, and Pliocene, were unequal in length, so they have been variously divided or left undivided to obtain ten approximately equal divisions of the Tertiary Period (about 70 million years). These so-called 'sub-periods' are labelled as—upper and lower Pliocene (UP, LP); upper, middle and lower Miocene, (UM, MM, LM); Oligocene; upper, middle and lower Eocene (UE, ME, LE); and Paleocene (Pa). The Oligocene is probably the longest of these sub-periods, and the corresponding diatoms are all from New Zealand: these records may include some lower Miocene species but they are mainly from deposits still accepted as Oligocene. Except for this, each sub-period is regarded as covering about one-tenth of 70 m.y. or about 7 ± 1 million years. Knopf has very recently pointed out that about 10 million years should be added to the normal 60 m.y. to account for the Paleocene epoch before lower Eocene began. Simpson at first subtracted 15 m.y. from 60 m.y. and got 45 m.y. for Tertiary since the beginning of Eocene but now he uses a longer time-scale.

On this basis of ten sub-periods the numbers of new and old species and genera can be counted in the accumulated published records for all known deposits of Tertiary diatoms.

Many of the arithmetical results of this counting have been analysed and published to some extent in a series of papers (Q.E. VII–XVIII). One of the main results has been the new emphasis on long-lived species as well as genera which were recognized at the beginning of stratigraphy by William Smith. Quoting from Holmes, *Principles of Physical Geology*—'He (Smith) found that while some of the fossils in any particular bed might be the *same* as some of those from the beds above or below, others were definitely distinctive'.

Another of the main results concerns time-rates for the appearance of new forms of specific or generic status. The number of new forms of any category at or above species rank arising during any one sub-period has depended upon, or has been a function of, two dominant factors. These are (*a*) the number of old units already in living existence within the category and (*b*) the age of the group concerned.

Since the old long-lived species and genera have mainly tended to be permanent up to Recent time, the other type of evolutionary change, namely extinction, has been of subsidiary importance in producing permanent evolutionary changes, although the early extinction of a large proportion (from 7/16ths to 12/16ths) of new species has increased the total change in groups of species from one sub-period to another, even between two successive sub-periods.

Putting this briefly—(*a*) *the number of new forms has increased geometrically* on a uniform time-scale, and (*b*) this number has depended upon the previous history of the group in so far as new groups have generally increased in their number of diverse kinds (species and genera) but this increase has ceased, gradually or abruptly, after the group (genus or family) has attained a critical age. Very old genera tend to produce fewer new species than they did in their earlier stages, and the same applies to families, but even in young, actively developing genera the rate for production of new species has seldom exceeded one for each available old species in 3 to 7 million years.

The geometrically progressive increase in numbers is well established for many groups of plants and lower animals. The known history of such groups, including the Termites, is usually in accordance with the general arithmetical history of diatom species and genera. The number of new species, or new genera, appearing in any one period of time has been a function of the number continuing from previous periods of time into the sub-period considered for origins of new forms.

There is no evidence in diatom history that the rate of appearance of new species or new genera has depended upon the number of individual organisms, an assumption which is commonly made by many mathematical theorists, who rely upon chance to supply their pabulum—but 'chance' is merely an accumulation of unanalysed causes, whereas in diatom history the numerical regularities have been analysed inductively and have demonstrated a number of controlling factors for observed increases and decreases.

These factors can be specified as follows :—

(1) The rate of increase in the number of species in any one genus tends towards a geometrical progression during the early history of the genus, for about 50 million years or more. The rate for residual increase has been $\times 1{\cdot}25$ per 7 m.y. for centric diatoms and $\times 2{\cdot}0$ per 7 m.y. for allogamous pennate diatoms. This has meant that whereas the number of species has doubled more or less in each sub-period for the pennate genera, it has taken 3 sub-periods or about 20 m.y. for the doubling of the number of species in centric genera. This residual increase does not include the short-lived species.

(2) After its first stage of relatively rapid increase, each genus has, gradually or abruptly, ceased to produce new long-lived species and has produced only a few, if any, new short lived species. At this stage the genus does not *increase* in size and it is *maintained* in living existence only by the persistence of its later long-lived species. Recently found examples in other groups may be indicated by *Metasequoia* and *Latimeria*.

(3) Younger genera, by their first stages of increase, have maintained the rates of increase for both groups of diatoms at about the same values as those found for the earlier or older genera.

(4) Present generic size, as number of living species, has been controlled by :

- (*a*) the *actual* age of the genus in millions of years :
- (*b*) the *relative* age of the genus as measured by its four stages of initial lag, primary expansion, maintenance, and senescence :
- (*c*) the proportion of long-lived species which have continued into sub-periods subsequent to the one of origin, and have thus been present to act as parental species for later progeny.
- (*d*) the degree of mutability within the morphological limits defining the genus : a few living monotypic genera are known in which the one original species has given rise to no new species during its 50 million years existence.

Summarizing the actual time-rates as intervals between the sudden origins of new species and new genera of diatoms, and relating the numbers of these origins to the available parental species and genera—

(*a*) the rate for species-production per unit old species present has been in Centrales about one new species for each old species in from 3 to 14 million years, with about three-quarters of the new species short-lived; while in the allogamous pennate families the rate has been nearly 2 new species for each old species in about 7 million years, with one out of each two new species short-lived.

(*b*) the rate for production of new genera has been about 0·24 and 0·64 per 10 m.y. for the same two groups of diatoms, and this means that for each old genus available as a parent genus, one new genus has arisen in about 30 m.y. in Centrales and in about 10–12 m.y. in allogamous Pennales.

The slowness of evolutionary changes in the mainly marine diatoms with mainly uniparental muliplication should not obscure the essential fact that even under these conditions evolutionary changes have actually taken place and have done so with a considerable degree of regularity.

Two large evolutionary changes may be noted in diatom history. The first is the development of bilateral symmetry, which has been shown by D'Arcy Thompson to be almost inevitable because of the delicacy of balance required for complete radial symmetry: this abrupt difference in symmetry has arisen several times in different lineages. The second change was more fundamental and may have occurred only once, as one of Sewall Wright's non-recurrent mutations, an 'aromorphosis' in Sewertzoff's terminology, namely the acquirement of some degree of motility of the individual organism. This change made possible both occasional biparental reproduction, and also the invasion of brackish and freshwater habitats and even of soil surfaces on dry land by the actively moving allogamous pennate types. There is no time-rate for such an isolated non-recurrent phenomenon, but it was the most strongly differentiating evolutionary change in the whole of diatom history.

Summarizing diagrams and Tables were used as lantern-slide illustrations to show some of the numerical facts and some parts of the analyses which have been made.

GEOLOGISCHE ZEIT UND ORGANISCHE ENTWICKLUNG

Von Otto H. Schindewolf, Tübingen.

(Mit 2 Abbildungen.)

Die heute gebotene Möglichkeit, absolute, wenn auch zunächst nur größenordnungsmäßig angenäherte Zeitzahlen in die Analyse stammesgeschichtlicher Abläufe einzusetzen, macht die Phylogenie einer quantitativen Behandlung zugänglich. Es lassen sich auf diese Weise zahlenmäßig begründete Vorstellungen über die Geschwindigkeit bzw. Langsamkeit der Stammesentwicklung gewinnen und daraus weiterhin Folgerungen auf die Ablaufsformen des stammesgeschichtlichen Wandels und ihre Deutung herleiten. Erste Anläufe zur Erschließung dieses neuen Forschungsgebietes sind von G. G. Simpson (1944, 1949) J. Small (1948, 1950) und F. E. Zeuner (1946, 1949) unternommen worden; es verspricht für die Zukunft eine reiche Ernte und eine wertvolle Ergänzung unserer stammesgeschichtlichen Auffassungen.

Auf Grund zahlreicher paläontologischer Befunde kann es heute als eine gesicherte Tatsache gelten, daß zu Beginn eines jeden stammesgeschichtlichen Zyklus, gleichgültig welcher Größenordnung, eine starke Beschleunigung der

Evolution vorliegt, die in kurzer Zeitspanne große Umbildungseffekte hervorbringt, während in späteren Phasen des betreffenden Zyklus die Entwicklungsgeschwindigkeit wesentlich geringer ist und die Umbildungsfähigkeit erlahmt.

Ein ausgezeichnetes Beispiel dafür bildet die *stammesgeschichtliche Entfaltung der plazentalen Säugetiere* im Alttertiär (Abb. 1). In der Oberkreide treten uns die Insectivoren als ältester und niederster Stamm entgegen, die den großartigen Entfaltungszyklus der Eutheria einleiten. An der Kreide/Tertiär-Grenze und im älteren Paleozän spalten sich alsdann von diesem Primärstamme unmittelbar oder mittelbar die sämtlichen Ordnungen der Plazentalier ab, die wir überhaupt kennen. 25 Ordnungen, die gesamte Formenfülle der Infraklasse repräsentierend, erscheinen in dem relativ kurzen Zeitabschnitt von insgesamt 10-15 Mill. Jahren schlagartig auf der Bildfläche, während in der etwa 60 Mill. Jahre dauernden nachpaleozänen Geschichte der Säugetiere nicht eine einzige neue Ordnung mehr hinzukommt !

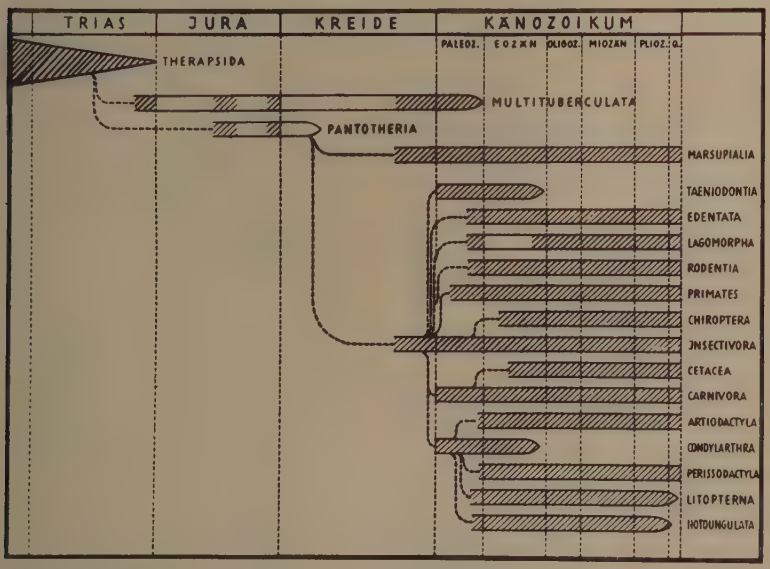

ABB. 1.—Entfaltungsbild der Eutheria an der Kreide/Tertiär-Grenze. Die durch Fossilien belegten Abschnitte der Stämme sind durch Schraffur gekennzeichnet.

Selbstverständlich steht auch da die Entwicklung nicht still. Es findet eine starke Vermannigfaltigung der Formen statt; zahlreiche Sonderspezialisierungen und -anpassungen im Rahmen der Ordnungen werden erworben, es erfolgt eine Aufgliederung in Familien, Gattungen und Arten, aber ein größerer stammesgeschichtlicher Umbildungsschritt vom Range einer Ordnung tritt später nicht mehr ein. Die grundlegenden Baugefüge sämtlicher Ordnungen werden an der Basis des neuen Entwicklungszyklus hervorgebracht, der mit der Einführung der Plazentalier-Organisation beginnt. Wir haben hier eine Periode hochgesteigerter Entwicklungsintensität, weit ausgreifender und tief eingreifender Aufspaltung.

Sehr bemerkenswert ist dabei, daß die typischen Merkmale der einzelnen Ordnungen, beispielsweise der Fledermäuse, der Wale, Gürteltiere usw. von Anfang an vorliegen, wenn auch selbstverständlich nicht überall in der heutzutage erreichten vollen Ausdifferenzierung, so doch aber in ihren maßgebenden

Grundzügen. Der Aufbau der die Ordnungen kennzeichnenden Organisationsgefüge ist also mit außerordentlicher Beschleunigung vor sich gegangen, um ein Vielfaches schneller als ihr anschließender verhältnismäßig geringfügiger Ausbau. G. G. Simpson (1944) hat das am Beispiel der Fledermäuse veranschaulicht, die uns mindestens seit dem Mitteleozän mit abgeschlossenem Bauplan entgegentreten. Die für ihn bezeichnenden Flügel haben während des seither verstrichenen Zeitraums von 50-55 Mill. Jahren keinerlei nennenswerte Veränderungen mehr erfahren ; lediglich einige der nicht mehr funktionellen Elemente sind rückgebildet worden. Wenn die gleiche niedrige Entwicklungsrate, die für diese unbedeutenden Umbildungen gilt, auch für die Herausgestaltung des bauplantypischen Flügels aus der normalen Säugerhand maßgebend gewesen wäre, müßte der Beginn dieser Entwicklung nach einer Überschlagsberechnung von Simpson noch vor dem Ursprung der Erde liegen !

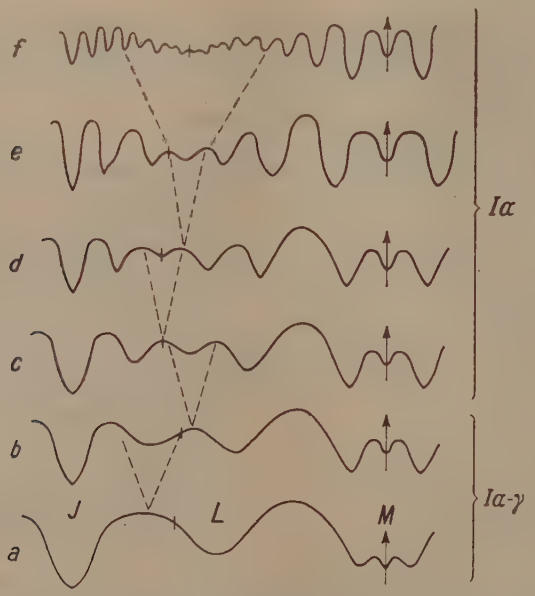

Abb. 2.—Explosive Entwicklung der Lobenlinien bei den Manticoceraten-Gattungen. *J*=Internlobus, *L*=Laterallobus, *M*=Mediansattel. Die Gattungen mit den unter *Iα* zusammengefaßten Lobenlinien finden sich nur an der Basis der Zone Iα des tiefsten Oberdevons, die anderen sind in den Zonen Iα—I*γ* vertreten.

Um nur ein weiteres Beispiel noch herauszugreifen, das uns ganz analoge Verhältnisse bei einem Entwicklungszyklus von geringerer Amplitude vor Augen führt, verweisen wir auf die *explosive Entwicklung der Goniatiten-Familie Manticoceratidae* im untersten Oberdevon. Diese Familie zeichnet sich gegenüber ihrer Stammform in der Lobenlinie durch den Erwerb eines Mediansattels aus, eines durchgreifend neuen, für die Taxonomie und, wie das stammesgeschichtliche Verhalten lehrt, auch für die Phylogenie der niederen Ammoneen sehr bedeutungsvollen Merkmals. Auch hier wieder hat sogleich nach der Emergenz der neuen Organisation eine starke Aufspaltung und Entwicklungsbeschleunigung eingesetzt. Die neue Familie tritt uns an der Basis des Oberdevons mit nicht weniger als 6 Gattungen entgegen, die eine sehr verschiedene Entwicklungshöhe der Lobenlinie aufweisen (Abb. 2*a–f*). Durch

eine gesetzmäßige Aufspaltung des Innensattels vermehrt sich die Zahl der Loben-Elemente in der Gesamtlobenlinie von ursprünglich 6 bei der Ausgangsform der Entfaltung bis auf 34 bei der Endform. Den einzelnen Entwicklungsstufen der Lobenlinie wird der Rang von Gattungen beigemessen, und alle diese Gattungen mit sehr erheblichen Umbildungsbeträgen sind in dem Teilabschnitt einer einzigen Goniatitenzone, d. h. während eines Zeitraums von größenordnungsmäßig höchstens $\frac{1}{2}$ Mill. Jahren, entstanden. Die am höchsten differenzierten Glieder (Abb. 2*c–f*) dieses überstürzten Entwicklungsprozesses sterben alsbald nach ihrem Erscheinen wieder aus; nur die einfachen Ausgangsgattungen (Abb. 2*a–b*) leben in den folgenden Zonen während einer Zeitspanne von etwa 3 Mill. Jahren noch fort, bleiben gattungsmäßig, d. h. in der Organisationshöhe der Lobenlinie, konstant und bringen in langsamer Ausgestaltung lediglich noch geringfügige artliche Unterschiede in der Gehäuseform und Skulptur hervor. Wenn wir diese allmähliche, langsame Artumbildung als die normale Entwicklungsrate ansetzen, so wird sie am Beginn der phyletischen Entfaltung der Familie bei der Bildung der Gattungen völlig überrannt.

In einem jeden stammesgeschichtlichen Zyklus lassen sich also zunächst 2 Phasen unterscheiden, die durch eine abweichende Geschwindigkeit und verschiedene Art der Evolution gekennzeichnet sind. Ich habe sie 1) die Phase der *Typogenese*, der Herausgestaltung der Grundbaupläne, und 2) die der *Typostase*, des unverändert beibehaltenen Typengefüges, genannt. Ihnen schließt sich als Endabschnitt 3) die Phase der *Typolyse*, der Auflösung des Bauplangepräges vor dem Aussterben an.

Man hat in dieser Darstellungsweise ein Gedankenrelikt der idealistischen Morphologie sehen wollen, die heute überwunden sei. Dazu habe ich zu bemerken, daß m.E. die vergleichende Morphologie (wie ich sie unter Ausscheidung der zeitbedingten metaphysischen Zutaten der idealistischen Epoche lieber bezeichnen möchte) als wichtige Grundlage der Biologie und als das uns allein zugängliche Ausdrucksmittel der Phylogenie unentbehrlich ist und bleibt, also überhaupt nicht überwunden werden kann. Man mag die Dinge wenden, wie man will; man kommt um die grundlegende Tatsache nicht herum, daß, rein phylogenetisch betrachtet, die einzelnen Merkmale der Organismen eine abgestufte Veränderlichkeit zeigen, daß es einmal Merkmale gibt, die eine mehr oder weniger lange Zeit hindurch konstant oder quasi-konstant bleiben und dementsprechend einen mehr oder weniger umfangreichen Formenkreis kennzeichnen, und andere, die sehr labil sind und in ihrer jeweiligen Prägung nur kleinste Formengruppen charakterisieren. Die letzteren sind die Artmerkmale, die anderen die Eigenschaften der übergeordneten Kategorien, der stufenweise umfassenderen Baupläne oder kurz der Typen.

In welcher Weise ist die auffallende Entwicklungsbeschleunigung in der Phase der Typogenese oder der Quantenevolution, wie Simpson sie nennt, zu deuten? Lücken oder sonstige Zufälle der Überlieferung sind auszuscheiden, wie hier leider im einzelnen nicht begründet werden kann. Wir dürfen und müssen in zahlreichen kritisch geprüften Fällen annehmen, daß einigermaßen getreue Abbilder der tatsächlichen stammesgeschichtlichen Gegebenheiten vorliegen.

Man hat versucht, die Entwicklungsbeschleunigung am Beginn der stammesgeschichtlichen Zyklen damit zu klären, daß die Frühformen, entsprechend der Regel der phylogenetischen Größenzunahme, kleinwüchsig waren und damit zusammenhängend eine raschere Generationenfolge zeigten, welche die Wirksamkeit der Selektion erhöhte. Der fossile Stoff unter Berücksichtigung des Zeitfaktors lehrt indessen (Zeuner, 1931, Simpson, 1944), daß offensichtlich die Generationsdichte ohne Einfluß auf die stammesgeschichtliche Entwicklungsgeschwindigkeit ist.

Ferner ist angenommen worden, daß die Populationen zu Beginn eines neuen Entwicklungszyklus zunächst sehr klein waren und daß dementsprechend ein hoher Selektionsdruck herrschte. In vielen Fällen trifft nachweislich diese Voraussetzung nicht zu. Faktoren der Populationsgenetik mögen mitspielen, sie reichen jedoch zu einer vollen Deutung nicht aus.

Ungenügend ist auch die Vorstellung, die basale explosive Entwicklung sei durch eine Besiedelung ökologisch unbesetzter Räume oder Nischen bedingt, wodurch die Selektionswirkung erheblich gesteigert worden sei. Auch diese Prämisse ist durchaus nicht überall erfüllt. Im übrigen würde dadurch allenfalls die Vermannigfaltigung der Stämme und ihr Aufblühen verständlich. Nicht zu erklären aber ist damit der wesentlichste Punkt, nämlich die Herausgestaltung der grundlegend neuen Bauplan-Organisation, die jeweils zu dieser Besiedelung neuer Räumer überhaupt erst befähigte.

Auszuschneiden ist endlich der Gedanke einer etwaigen Erhöhung der Mutationsrate. Die nachteiligen Mutationen würden dabei überwiegen, das ausgewogene Verhältnis von Mutabilität und Selektion nach der negativen Seite hin verschieben und zweifellos zu einem Eignungsverlust führen.

Es bleibt daher, soweit ich sehe, zur Deutung der typogenetischen Phase mit Quanten-Evolution nur die Annahme eines größeren Ausmaßes, bzw. Effektes der einzelnen Mutationsschritte (evtl. unter akzessorischer Mitwirkung einiger der soeben genannten Faktoren). Ich rechne dementsprechend mit Mutationen, einzelnen oder kurzen Ketten von solchen, die in das Grundgefüge des Bauplans selbst eingreifen, diesen in kurzen Zeitspannen umgestalten und dadurch der Evolution auf der nunmehr veränderten Grundlage zahlreiche neue Einzelwege erschließen. Von paläontologischen Befunden ausgehend und in ähnlicher Weise wie Zeuner, gelangen wir damit zu durchaus ähnlichen Folgerungen und Forderungen, wie R. Goldschmidt und später auch andere Genetiker (H. Burgeff, W. Ludwig, H. Stubbe & F. v. Wettstein) sie von vererbungstheoretischen Gesichtspunkten aus erhoben hatten.

Zum mindesten rein begrifflich wird man die Mutationen, die tief in das Grundgefüge eingreifen, sich gewöhnlich in frühen ontogenetischen Stadien äußern und alsdann eine Reihe korrelativer Abänderungen nach sich ziehen, also eine sehr einschneidende Gesamtwirkung haben, von denen unterscheiden müssen, die nur ein relativ belangloses, für den Organisationsplan völlig unwesentliches Merkmal, wie etwa eine bestimmte Farbnuance oder die Länge einer Borste betreffen. In früheren Arbeiten habe ich in Übereinstimmung mit manchen Genetikern die Mutationen, die m.E. für die typogenetische Phase zu fordern sind, schlechthin "*Grossmutationen*" genannt, wobei ich lediglich ihren höhern Wirkungsgrad gegenüber den effektarmen Kleinmutationen im Auge hatte. Mit R. Goldschmidt mag man sie aber auch als "Systemmutation" oder mit W. Ludwig als "Schlüsselmutationen" bezeichnen, die der Evolution entscheidend neue Wege erschließen.

Unter den fossilen Wirbellosen gibt es gewisse von mir veröffentlichte Beweise dafür, daß ein einziger, in frühen ontogenetischen Stadien einsetzender Umbildungsschritt genügt, einen durchgreifend neuen Bauplan einzuleiten und damit der Entwicklung neue Wege zu eröffnen. Meist beruhen diese Umstellungen darauf, daß in der Ontogenese einer Form eine Entwicklungsrichtung eingeschlagen wird, die sich grundsätzlich, alternativ von der bisherigen unterscheidet und damit allmähliche Übergänge ausschließt. Zwischen den Repräsentanten derartiger verschiedener Entwicklungsrichtungen gibt es demgemäß keine Bindeglieder, die etwa unter Addition kleiner Anpassungsschritte, auf dem Wege gleitender Artbildung die Bauplangrenze überbrücken würden.

Damit soll natürlich nicht behauptet werden, daß ein neuer, ungeheuer komplizierter Bauplan in seiner Gesamtheit und mit allen seinen Einzelzügen auf einen Schlag entsteht. Der oft kolportierte und ins Lächerliche gezogene Satz

W. Garstang's :" " Der erste Vogel kroch aus einem Reptilei " ist selbstverständlich nur symbolisch gemeint und nicht wörtlich in dem Sinne aufzufassen, daß der gesamte ausdifferenzierte Bauplan, wie ihn die heutigen Vögel verkörpern, plötzlich, in einem einzigen Umbildungsschritte aus einem womöglich einseitig spezialisiert gedachten Reptil nach dem Muster rezenter Vertreter geschaffen sei. Es geht vielmehr lediglich um den ersten Entwicklungsschritt, der die neue Organisation anbahnt und, wie das stammesgeschichtliche Verhalten beweist, eine große evolutorische Bedeutung hat. Ferner ist es selbstverständlich, daß die ersten Vertreter einer neuen Entwicklungsrichtung neben den veränderten Bauplanmerkmalen auch gewisse zum Leben notwendige Spezialisationen und Anpassungen (Präadaptationen) besessen haben müssen. Da ich das früher selbst wiederholt hervorgehoben habe, sind die von Simpson gegen mich in dieser Hinsicht erhobenen Einwände gegenstandslos.

Zu der Frage nach der Natur der " Großmutationen ", auf welchen Veränderungen der Genome sie beruhen, ob sie nur quantitativ oder auch qualitativ von den Kleinmutationen verschieden sind, kann der Paläontologe nichts beitragen; er muß diese Frage dem Genetiker zur Beantwortung überlassen.

Summary.

Palaeontological evidence suggests that the beginning of each phylogenetic cycle, irrespective of the systematic category concerned, is marked by an intensification of evolution. In the later phases, the rate of evolution is much smaller and the ability to change decreases. An instructive example is the evolution of the placental mammals in the early Tertiary. In the upper Cretaceous the Insectivora appear, initiating the evolutionary cycle of the Eutheria. At the boundary of Cretaceous and Tertiary, and in the early Paleocene all other known placental orders become differentiated from the original group. Twenty-five orders, representing the entire morphological range of the subclass, appear in the relatively short period of 10–15 million years, whilst during the subsequent, post-Paleocene, period of 60 million years not a single new order is added.

Evolution, of course, is not arrested in this second period. Specialization and adaptation continue within the framework of the orders, which split up into lower systematic categories. The chief features of the organization of orders, like the whales, or the bats, or the armadillos appear already at the beginning of the cycle.

The upper Devonian Cephalopod family Manticoceratidae acquired a median saddle in its suture-line. Once more, intense splitting occurred at the very beginning, and within the very short period of a sub-division of a Goniatite horizon, of the duration of perhaps half a million years, at least 6 genera were formed. The most highly specialized types, however, soon became extinct, but the simpler genera survived through a period of about 3 million years without change except in insignificant specific characters.

A phylogenetic cycle therefore, comprises three phases, the first and rapid one of *typogenesis*, the drawn-out second one of *typostasis*, and a final one (not here discussed) of *typolysis* or disintegration of the structural characters which precedes extinction.

The typogenetic phase is Simpson's ' quantum evolution ' and Zeuner's ' explosive phase '. How can it be explained ? Stratigraphical sequences of fossiliferous deposits are so complete that, in the cases considered, gaps in the palaeontological record have to be ruled out. It has been suggested that early forms were often of small size, and thus would have had a more rapid succession of generations increasing the effects of selection. But since Zeuner demonstrated

as long ago as in 1931 and as Simpson rediscovered independently in 1944, that the number of generations appears to have little effect on phylogenetic evolution, this explanation has to be abandoned. Another interpretation assumes very small populations with high selection pressure at the beginning of an evolutionary cycle. This is a possibility, but in many investigated cases it does not apply. Similarly, occupation of ecological niches or empty spaces, with increase in the effects of selection, is conceivable, but the condition that niches are available is often not fulfilled. An increase in the rate of mutation does not afford a satisfactory explanation either, since in such process disadvantageous mutations would preponderate, shift the balance of mutability and selection to the negative side and undoubtedly lead to an overall loss in adaptive efficiency.

Thus, there remains only the assumption of an unusually large size (or effect) of the mutational steps. Single mutations or short series of mutations would interfere with the essential elements in the organization, and therefore change it in a short time and present the processes of natural selection with an altogether new type of organization. They have been called '*Grossmutationen*'. Starting from palaeontological evidence one thus arrives at conclusions not unlike those of the geneticists.

GENERAL DISCUSSION

In opening the discussion the PRESIDENT remarked that the zoologists were in a more fortunate position than the botanists because the materials with which they dealt were in the main macroscopic and because the geological record was more perfect. Diatoms required a laborious microscopic examination and the data relating to their past history were very scanty. One could admire the industry and energy which Professor Small had exhibited, but the basis of fact in support of his thesis was open to grave suspicion. The number of deposits of fossil diatoms so far examined was very small, although it might perhaps be conceded that they furnished something of the nature of a cross-section. There were, however, far more serious objections. The bulk of the deposits so far examined were of marine origin and consisted essentially of planktonic forms. The rich diatom flora existing between tide-levels and the numerous bottom-living forms would hardly appear in such deposits so that the picture they furnished was probably very one-sided. Preservation of a diatom depended on the degree of silicification of the wall, and it might be questioned whether it was justifiable to assume that silicification of the diatom-wall had always been as extensive as at the present day. Even among living diatoms there were a considerable number of species (*e.g.* some of those of *Licmophora*, *Rhizosolenia*, and *Nitzschia*) in which silicification was feeble, and it was possible that in the past such instances had been more frequent.

In relation to diatoms the problem of what is a species was very acute. Opinions among authorities differed widely as to the status of many diatoms and as to their reference to one genus or another. Finally, objection might be taken to the treatment of the Fragilariaceae as a group distinct from other Pennales, since recent work had shown that two of the Fragilariaceae, at least, formed their auxospores by a process of sexual fusion between distinct individuals as in other Pennales.

Mr. F. J. MANNING: Professor Zeuner has referred to some recent work on the cytology of the Honey Bee (*Apis mellifera* L.). Secondary and also quadruple association of chromosomes was observed during meiosis. As to the chromosome numbers of Recent Meliponini and Apinini the haploid set of the former is $n=9$, according to Kerr, 1948, and that for the latter $n=16$. The number is still unknown for the Bombini. It would seem, therefore, as though the common Eocene ancestor of Apini and Meliponini, *Chalcobombus*, had $n=8$.

The basic number for hymenopterans is believed to be 4. This number was very strongly suggested by the comparative study of the chromosome numbers of over 70 species of Hymenoptera from many diverse genera.

The evidence from related groups renders it probable that the association of chromosomes in *Apis* is due to polyploidy, and that it has a phylogenetic significance. The genetic formula for the Meliponini may therefore be written $n=2x+1=9$, and that for the Apini $n=4x=16$.

Returning to the palaeontological aspect, the direct ancestor of the Apini belongs to the Eocene genus *Electrapis*, with several species, and which is regarded as the descendant of *Chalcobombus*. As Professor Zeuner has pointed out, its evolution in body morphology up to the Upper Oligocene was considerable, at which stage it became very close indeed to Recent *Apis*. But thereafter the morphological evolution was extremely slow. This possibly suggests that the last polyploidy of the Apini occurred between the Eocene and the Oligocene.

Mr. R. Ross :

In the papers which Professor Small (1945 A & B, 1946, 1948 A & B, 1949 A & B, 1950) has published recently, and again in the course of to-night's discussion, he has stated that the fossil history of the Diatoms is inconsistent with the neo-Darwinian explanation of the mechanism of evolution. In his view this history demonstrates that, in this group, species must arise by 'one-step specific mutation, an instantaneous nuclear change in one living unit' (Small 1946, p. 69) The argument by which he comes to this conclusion is the distinct delimitation of the species of fossil Diatoms, with intermediate forms almost completely unknown, and the fact that their duration is either long or short, and the proportion of long-lived to short-lived species is more or less constant, and their duration is therefore pre-determined at the moment of origin of the species. In my opinion the three main foundations of Small's arguments are not, as he considers, facts but unjustified assumptions. Owing to the great theoretical importance of Small's views, I have felt impelled to take this opportunity of setting out my reasons for holding this opinion of the bases of his views.

Small's basic assumptions are :—

(1) that the Diatoms are a well monographed group. 'Lists of genera and species which have been the subjects of balanced judgments by one expert for each list [include] Diatoms (Mills 1933–5).' (Small 1946, p. 57.)

(2) that the fossil species of Diatoms are mostly distinct and without intermediate forms. 'There are 2720 fossil species of Diatoms; at least 2600 of these are quite distinct, readily determined species with no intermediate forms between the specific unities; there are 2600 fossil species of diatoms *which neither have nor have had intermediate stages in their origins.*' (Small 1948 A, p. 296, original italics.)

(3) that our knowledge of the occurrence and duration of diatom species during the Tertiary is virtually complete. 'The diatoms, by means of their patterned shells of naturally indestructible non-colloidal silica, have left a geological record which is known to such a degree of completeness that the arithmetical values form a basis for general rules-within-limits, which can be demonstrated as arithmetical facts.' (Small 1946, p. 53.)

Mills' *Index to the Genera and Species of the Diatomaceae* (1933–5) is little more than its title suggests. Whilst it does, like the original *Index Kewensis*, purport to be a nomenclator as well as an index, the opinions expressed in it as to the status of species and genera are only very rarely the result of Mills' own judgement. Normally he follows the last reputedly authoritative account which dealt with the species concerned. This is often De Toni (1891–4) where the author's own conclusions are recorded, but these are based mainly on published descriptions and figures rather than on study of the diatoms themselves, and the

work can scarcely be regarded as of monographic status. Where there is division of opinion on the validity of a genus, Mills does not decide. Species are printed in capitals, indicating a valid name, under both *Triceratium* and *Biddulphia*, and those shown as valid under *Caloneis*, *Diploneis*, *Pinnularia* and *Schizonema* mostly appear as valid under *Navicula* also.

Very little monographic work has been done on the Diatoms during this century and only a few small genera have been dealt with. Almost the whole group is in need of monographic revision, and I consider that the currently accepted generic limits of one third of the genera containing more than forty species are at variance with a natural arrangement of the group. *Actinoptychus* Ehrenb., which is one of the two genera which Small (1948 A) has chosen to exemplify a typical generic history, has never been monographed, and its species are in the state of confusion which any taxonomist would expect in an unrevised and difficult genus of 170 species.

Since Mills' Index was published only one generic revision has appeared, that by Swatman (1948) of the small fossil genus *Fenestrella* Grev. He showed that *Janischia* Grun. apud Van Heurck should be included in it and also that one of the species previously regarded as a *Fenestrella* is actually a *Raphoneis*, a genus in a different family. During the publication of the Index, but after the part dealing with *Arachnoidiscus* Deane ex Pritchard had appeared, N. E. Brown (1933) published a monograph of that genus. In this he retained as valid only seven of the ten accepted species but added twenty new ones. I have just completed a monograph of the genus *Rutilaria* Grev. which is to be published in *Bull. Brit. Mus.* (*Nat. Hist.*), *Bot.* In this I show that *Syndetocystis* Ralfs ex Grev. and *Syndetoneis* Grun. ex De Toni must be combined with *Rutilaria* Grev. The nineteen valid species which, according to Mills, are contained in these three genera are reduced to nine and a hitherto undescribed one added. These three revisions of small genera illustrate the magnitude of the changes which would result from monographic treatment throughout the whole group, and indicate how inadequate is the taxonomic basis of Small's work and how invalid his first assumption.

As regards the absence of intermediates, I have, in the course of this work on *Rutilaria* Grev., examined about 1000 specimens of the genus. Almost all these fall into clear cut species, but among them are two from the Oligocene which are intermediate between two closely related species, one with a history extending from the Paleocene to the recent and the other known only from the Miocene.*

Swatman (1948) mentions an Oligocene specimen intermediate between the Paleocene to Miocene *Fenestrella barbadensis* Grev. and the Oligocene to Miocene *F. convexa* Brun, and there is in the collection of the British Museum (Natural History) a Paleocene specimen intermediate between *F. barbadensis* Grev. and *F. russica* Swatman, which is found only in the Paleocene. In addition in work towards a revision of the section *Lyratae* of the genus *Navicula* Bory, in which I have so far considered only about twelve species, I find that, whilst *N. spectabilis* Greg. and *N. angelorum* Cleve are readily distinguishable in the Lower Pliocene deposits of Mexillones in Chile and the Upper Miocene deposits in California, there are intermediate forms in the Californian Middle Miocene which make it impossible to maintain any clear distinction between the two species at that period.

On the basis of neo-Darwinian theory it would be expected that, in a uniform and stable environment, a well adapted genetic pattern would show long periods of stability with the elimination of mutant genes by natural selection. Changes

* There is a division of opinion on the age of the diatom bearing Oceanic beds in Barbados, some authors, *e.g.* Jukes-Brown and Harrison (1892) and Frenguelli (1949), considering them as Miocene, and others, *e.g.* Senn (1940) as Upper Eocene. Small adopts the latter view. In this paragraph their Miocene dating is accepted since the evidence from the diatoms seems to favour this.

in genetic pattern, initiated either by change in environmental conditions or by the arising of a mutant gene or genes giving sufficient competitive advantage, would occur infrequently. During such changes there would be genetic instability which would cause them to proceed comparatively rapidly until a new pattern of compatible and mutually advantageous genes had been established and a new species evolved. These changes would normally be restricted to a small and localized part of the whole population of the parent species until the new genetic pattern was established. Accordingly a continuous and world-wide fossil record would be necessary if they were all to be detected. This, as is pointed out below, we have not got. Furthermore, it is only during the detailed examination of a group for revision purposes that intermediates are likely to be recognized as such, for only then are the limits of species under consideration. In floristic works, which comprise most of the papers giving information on the geographical and geological distribution of diatoms, such intermediates are usually recorded as ——— sp., or the author plumps for one of the species between which the specimen is intermediate. This makes these observed occurrences of intermediates as many as neo-Darwinian theory would lead one to expect.

Table I

	No. of species recorded		Fossil Deposits	
Sub-period	Max.	Min.	No.	Locality
C	154	154	2	California ; Germany.
Pa	335	331	1	Volga Basin, Russia.
LE	184	93	2	Denmark ; England.
ME	128	31	1	California.
UE	526	429	2	Barbados ; Haiti.
O	432	278	1	New Zealand.
LM	650	436	5	Atlantic Coast, U.S.A.; Oregon ; Mexico ; Moravia ; Japan.
MM	937	564	11	Atlantic Coast, U.S.A.; California ; Trinidad ; Greenland ; Hungary ; Spain ; Italy ; Malta ; Crimea ; Nicobar Islands ; Japan.
UM	707	232	5	California ; Hungary ; Sicily ; Japan ; France (f).
LP	1015	502	12	Hungary ; Bulgaria ; Spain ; Greece ; California (b) ; Eastern U.S.A. (f) ; Finland (f) ; Germany (f) ; France (f) ; Italy (f) ; Japan (f) ; Australia (f).
UP	773	13	4	Algeria ; Canada (f) ; France (f) ; Italy (f).

(b) brackish water, (f) freshwater, all others marine.

The silicious shells of Diatoms are not indestructible. This is pointed out by Reinhold (1937) who draws attention to their absence in a large percentage of samples of marine origin and suitable facies and points out that almost all the deposits in which well preserved Diatoms are found in quantity are interbedded with volcanic ash. This is the reason for the small number of localities from which we have records of fossil Diatoms, particularly in the Paleogene. Table I sets out, for each of the sub-periods into which Small (1945 B & passim) has divided Tertiary time, the numbers of species recorded and the number and locality of the deposits in which fossil Diatoms have been found. A series of outcrops of similar age and Diatom content in the same region are regarded as a single deposit. This table has been compiled from Small's (1945 B) own basic data with the exception that the additional records of Cretaceous species from Moreno, California (Hanna 1934, Long, Fuge & Smith 1946, Barker and Meakin 1945, 1946, 1947, 1948, 1949, Meakin & Brigger 1949) have been incorporated. Small's chronology has been accepted also except that the Kamichev deposit from Russia, which he assigned doubtfully to the Lower Miocene, has been included with the

other Russian deposits in the Paleocene. Reinhold (1945) has shown that it belongs to the same formation, as, indeed, its Diatom content makes plain. Small so presents his data that it is impossible to determine from it whether a species recorded from earlier and later sub-periods has been recorded from an intervening one. It is for this reason that maximum and minimum figures are given in the table, the maximum assuming that all such species are recorded and the minimum that none are. The actual figure must lie between the two and evidence presented below suggests that it is nearer the minimum than the maximum.

This table makes clear the great geographical limitations of our knowledge of the diatoms of each sub-period, especially in the Paleogene and the Upper Pliocene. Of particular significance here is the lack of deposits of the same type in the same part of the world in consecutive sub-periods. The only cases where these are found in as many as three consecutive sub-periods are all in the Neogene. They are :

W. Coast of U.S.A. and Mexico	marine	LM–UM
Japan	marine	LM–UM
Hungary	marine	MM–LP
France	freshwater	UM–UP

Whilst there is considerable variation in the numbers of species recorded from individual fossil deposits, from over 300 in the Paleocene of the Volga Basin and the Oligocene of New Zealand down to about 50 in the Californian Middle Eocene and less than 20 from the Lower Pliocene of the Zante Islands, Greece, it is clear that the number of species recorded from any sub-period is dependent rather upon the number of deposits containing fossil Diatoms known from that sub-period than upon the age of the sub-period. This was tested statistically. The sub-periods from Cretaceous to Lower Pliocene were numbered from one to ten, the upper Pliocene being rejected because of its very poor representation in the fossil record, and the number of species recorded from each sub-period was taken as being the minimum figure in Table I plus one third of the difference between the minimum and maximum figures.* If x be the number of species recorded, y the number of deposits known and w the number of the sub-period, the probabilities of Student's t for the partial correlation coefficients were, on the assumption of no correlation :—

for $r_{xw.y}$) $\quad P>0{\cdot}3, \ <0{\cdot}4,$
for $r_{xy.w}$) $\quad P>0{\cdot}05, \ <0{\cdot}1.$

At the present day only a limited proportion of species of Diatoms have a cosmopolitan distribution, and there is no reason for supposing that this has not always been so. Indeed, collections from the sea bed over an area as limited and as uniform as those in which in a single fossil deposit was laid down would only yield a number of species of the same order as that found in a single marine fossil deposit. The Diatoms as a group, however, had a world-wide distribution as marine organisms in Cretaceous times, as is attested by their presence in rocks of that period in Germany (Müller, 1912 ; Forti & Schulz, 1932), France (Deflandre, 1941), California (Hanna, 1927 *et al.*) and Queensland (Dun, Rands & David, 1901). Taking all these facts in conjunction, there seems no reason for believing that the marine Diatom flora was not as numerous in species throughout the Tertiary as it is at present, and at least 3000 recent marine species are known. There is certainly no definite evidence for rejecting that view, and if it is true our knowledge of the species living in any fossil sub-period does not extend to one quarter of those alive at the time.

Another indication of the inadequacy of the published information on the geological history of the Diatoms is given by the alterations in the figures for the durations of species which study of extensive collections reveals. The results of

* For justification of this see below, p. 146.

such studies are contained in Swatman's (1948) revision of *Fenestrella* Grev. and mine, as yet unpublished, of *Rutilaria* Grev. These are both small genera and I have supplemented the information which they provide by compiling a geological history of the genus *Aulacodiscus* Ehrenb. from both the literature, including papers published since Mills' Index (1933–5), and also the collections of the British Museum (Natural History). In doing this I have examined all those specimens which extend the geological range of a species beyond its published records and rejected any such extensions based on mis-identifications. Table II compares the frequency distribution of durations of species in these genera as shown by these recent studies with those in Small's (1945B) data which are based on published records up to about 1935. In *Rutilaria* Grev. and *Fenestrella* Grev. the differences are in part due to taxonomic changes. Small's data for *Syndetocystis* Grev. and *Syndetoneis* Grun. ex De Toni have been included in those for *Rutilaria* Grev., and those for *Janischia* Grun. apud Van Heurck in *Fenestrella* Grev. In *Aulacodiscus* Ehrenb. the changes are all due to the inclusion of recently published new species or to extension of the known geological history of species; none is due to the combining of species previously considered separate.

Table II

Frequency Distribution of Durations of Fossil Records.

No. of	*Aulacodiscus*		*Rutilaria*		*Fenestrella*	
sub-periods	Small	Ross	Small	Ross	Small	Swatman
0*	25	9	5	–	–	–
1	80	92	10	3	4	1
2	6	7	1	1	–	–
3	2	8	1	1	–	2
4	6	5	1	2	–	1
5	4	8	–	1		
6	3	7	–	–		
7	2	7	1	–		
8	5	12	–	1		
9	–	1	–	–		
10	1	1	–	–		
11	2	4	–	1		
12	–	2				

* Species with only recent records.

Ratio of short (1–2 sub-periods) to long (over 3 sub-periods) durations, *i.e.* Small's e/p ratio.

Aulacodiscus	Small 3·7	Ross 2·1
Rutilaria	Small 5·5	Ross 0·8
Total	Small 4·0	Ross 2·0

In drawing up Table II I have had to place some fossil deposits not included by Small (1945B) in his chronological table, as follows :—

The new Russian deposts, Kamichev, Singiliewsky, Carlovo and Inza are co-eval with those previously known (Reinhold, 1945) and are therefore Paleocene.

The fossil material dredged from the Bering Sea by U.S.S. 'Albatross' at her station 4029 H is Lower Miocene (Hanna, 1929).

The deposit at St. Laurent-la-Vernède, Gard, France, is Middle Miocene (Lefébure, 1935).

The deposit at Tiltil, Chile, is Upper Miocene, and that at Mexillones, Chile, is Lower Pliocene (Frenguelli, 1949).

In order that the figures should be comparable, I retained the Barbados deposit as Upper Eocene.

Table II shows that these studies have resulted in a great decrease in the proportion of species whose durations are short as defined by Small (1946), that is,

species known from only one or two sub-periods. The extent to which it has proved possible to extend the known geological range of previously described species is masked in the figures for *Aulacodiscus* Ehrenb. by the inclusion in the later ones of 25 recently described species almost all of which are still known from only one sub-period. However, the great reduction in the number of recent species with no fossil record will be noticed. Another significant point is the increase in the number of species with a known geological range of three sub-periods. The absence of durations of this length was regarded by Small (1946) as evidence of a clear cut division of species into those of long and short duration. It is noteworthy that only one of these ranges occurs in the Paleogene, whilst seven are from the Neogene and three overlap the Paleogene–Neogene boundary. Since the number of species in these three genera with their first records below the Miocene is three times as many as those with a fossil record beginning in the Neogene, there is a very considerable relative lack of known durations of three sub-periods for species first recorded in the Paleogene. It seems probable that this is the result of the much poorer fossil record of the Diatoms during that period, and in particular of the lack of deposits in the same region in consecutive sub-periods.

A further demonstration of the incompleteness of our knowledge of the fossil diatom flora throughout the Tertiary was provided by the data from which Table II was drawn up. For the three genera included therein, there are, excluding the Upper Pliocene, 244 cases where the existence of a species in a sub-period can be inferred from its being recorded in earlier and later sub-periods. In only 87 of these, that is, in only 36%, is the species actually known. This is the basis for the assumption made above when calculating correlation coefficients as to the number of species actually recorded for a sub-period.

We thus have a number of items of evidence which indicate that the published information on the fossil history of Diatoms is very fragmentary. These are :

(i) the small number of fossil deposits in each sub-period and the lack of any increase in numbers of species per deposit during the Tertiary, indicating that the marine flora, at least, did not increase appreciably in numbers of species during the Tertiary, together with the much smaller number of species known from any fossil sub-period than from the present day,

(ii) the large amount of unpublished information available by study of a few genera in a large collection,

(iii) the large proportion of known gaps in the fossil records of individual species in those genera.

On the basis of this evidence it is possible to say with some confidence that, for any particular sub-period, we have records of no more than one quarter of the diatoms alive during that sub-period, and for Paleogene sub-periods the proportion is considerably less. Thus Small's third basic assumption is shown to be unfounded.

One final point must be made. The increase in the proportion of species with a known fossil duration of three sub-periods which has resulted from a detailed study of three genera, and the distribution of these in time demonstrate, with little room for doubt, that the sharp division which Small's data show between species of long and short duration, and also many short durations themselves, are artefacts of the distribution, both geological and geographical, of our limited knowledge of the fossil history of the Diatoms. Small has demonstrated the occurrence of some regularities in the distribution of these artefacts. I would, however, submit that there is no justification for rejecting the neo-Darwinian explanation of evolution, which is built upon so large a structure of co-ordinated evidence, on the basis of regularities in a series of artefacts whose relation to reality is not only doubtful, but probably not close.

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In concluding the discussion the PRESIDENT said that he thought Professor Zeuner had sounded the right note and that great caution was essential in these matters. It was requisite to make a careful study of each group and to convince oneself that the fossil evidence was adequate.

NOTES ON CHAROPHYTES FROM BRITISH COLUMBIA

By G. O. Allen, F.L.S.

(With 3 text-figures.)

Dr. Edward Buckell, who died in November 1944 at the age of eighty-three, was an old friend of the late Mr. James Groves, F.L.S., having met him in the 'eighties and later also when he (E.B.) was living at Romsey, Hants.

Belonging, like his father, to the medical profession, Dr. Buckell also inherited his botanical tastes and used to join him and Groves on their botanical expeditions when the latter was working on the Flora of Hampshire. In 1913 Dr. Buckell left for Canada where he settled on an apple ranch at Salmon Arm in British Columbia.

At the suggestion of Groves he started to search for charophytes and sent his first specimens in 1928, finding also in that year a species that Groves considered new, viz. *Chara Buckellii*. Up to the time of Groves's death in 1933 he had forwarded some eleven gatherings, and at my invitation he has very kindly continued to send material, always in fluid, the last being received in 1940.

His collection, thanks to considerable assistance from his son, amounted in all to about fifty-seven gatherings comprising 11 species ; 2 *Nitella*, 1 *Tolypella* and 8 *Chara* including the new species ; a very noteworthy addition to the charophyte records from this area, being about half the total for the whole of Canada.

They were all found in the southern interior of British Columbia between latitudes 50° and 52° and between the Fraser River and Coast Range on the west, and the Columbia River and Rocky Mountains on the east.

Dr. Buckell did not consider the immediate neighbourhood of Salmon Arm a good district for charophytes as there are few moderate sized sheets of water, and the larger lakes, such as the Shuswap Lake, with its rocky shoreline of some 600 miles and the water level rising and falling many feet with the seasons, are poor collecting grounds. There are no permanent ditches, and in the rapid, mountain-fed streams that often dry up for part of the year, the water is too cold for vegetation.

That so many species were found is all the more creditable seeing that the enormous amount of work the fruit ranch entailed left Dr. Buckell all too little leisure for botanical studies. Though Mr. Ronald Buckell's work on insect pests for the Canadian Department of Agriculture took him over the whole province he too had little time to spare for charophyte hunting.

Many of the areas that Mr. Buckell visited on his entomological work in the dry interior of the province had extensive open grassland cattle ranges with many small ponds in which charophytes could be found, and it was he who actually made the first gatherings of the new species.

Mr. Ronald Buckell has also sent me twenty further gatherings from British Columbia (and six from Alberta) made in 1946.

He mentions that all these charophyte records fall into two biotic areas, the Humid Transition Zone and the Arid Transition Zone. The former is mountainous with much forest and contains mainly large lakes, such as Kootenay Lake, Arrow Lakes and the Shuswap Lake system, including Mabel Lake, with comparatively few ponds. The latter consists of the narrow hot Okanagan Valley, together with the interior plateau from Kamloops north into the Chilcotin River country, where the water of its many ponds, and some fair-sized lakes, is commonly alkaline.

This plateau area, as one might expect, is evidently particularly suited to charophytes. I quote, for example, Mr. Buckell's remarks about Bridge Lake as ' full of pure clear water for several square miles and its bottom, only a few feet under water, often solidly covered by great sheets of *Chara*.' He adds that

a number of lakes in the southern interior of British Columbia, with their extensive *Chara* beds which harbour fresh-water shrimps and aquatic insects are famous trout lakes: such spots also attract wild duck.

Key to Species.

NITELLA.	
Homoeoclemae (branchlets in a whorl all similar)	1. *N. flexilis.*
Heteroclemae (branchlets in each whorl of two kinds)	2. *N. clavata.*
TOLYPELLA.	3. *T. prolifera.*
CHARA.	
Haplostephanae (stipulodes in a single circle).	
Ecorticate	4. *C. Braunii.*
Corticate stem, branchlets ecorticate.	5. *C. Buckellii.*
Diplostephanae (stipulodes in a double circle).	
Haplostichous stem-cortex (one row of cortical cells to each branchlet).	
Dioecious	6. *C. canescens.*
Monoecious	7. *C. evoluta.*
Diplostichous stem-cortex (two rows of cortical cells to each branchlet)	8. *C. contraria.*
Triplostichous stem-cortex (three rows of cortical cells to each branchlet).	
Dioecious	9. *C. aspera.*
Monoecious.	
Primary and secondary cortical cells about the same breadth.	10. *C. globularis.*
Primary cortical cells much broader than the secondary	11. *C. delicatula.*

1. **Nitella flexilis** Ag.

Shuswap Lake, August and October 1935 and October 1938.
Monoecious, branchlets once forked, dactyls one-celled.
The plants were mostly in a sterile condition.

var. **nidifica** Wallm.

Bridge Lake, July 1939.

This variety differs from the type in the fertile whorls having much shorter branchlets and forming more or less dense heads. The plant bore both oogonia and antheridia.

2. **Nitella clavata** Kütz.

Shuswap Lake, October 1947 and October 1938.

Monoecious, dactyls one-celled. Heteroclemous, *i.e.* having branchlets of two kinds at the stem whorl, viz. accessory simple ones in addition to the once forked branchlets of the primary circle. This character is well illustrated in the *Fragmente* (Braun and Nordstedt), fig. 33.

3. **Tolypella prolifera** Leonh.

Shuswarp Lake, August 1937.

Monoecious, sterile branchlets simple, ultimate cell of all rays conical. The only N. American *Tolypella* with these features. T. F. Allen described *T. fimbriata* from L. Ontario as a separate species mainly on the ground of its smaller size and larger fruit but Groves found the fruit did not exceed the limit in British species and having seen Allen's original specimens I agree with Groves that it is not separable from *T. prolifera.*

4. **Chara Braunii** Gmel. (*C. coronata* Br.)

Shuswap Lake, October 1937: Macoun recorded it from Chilliwack Valley, B.C.

Monoecious, a single circle of stipulodes, entirely ecorticate. No other entirely ecorticate *Chara* has been found in N. America.

5. **Chara Buckellii,** sp. n.

Haplostephana (unistipulata) corticata (irregulariter diplosticha) dioecia. Caulis crassus, diplo- vel partim triplo-corticatus, corticis cellulis primariis ac secundariis fere aequalibus. Aculei omnino inchoati. Stipulodia longa et crassa (saepe deficientia). Ramuli verticillorum 8–10, ecorticati : segmenta 4–5, turgida. Bracteae 3–4 plerumque. Oogonia interdum solitaria, saepe gemina, alterum sursum alterum deorsum directum : oospora c. 800 μ longa, c. 450 μ lata. Antheridium solum ad primum nodum, c. 900–975 μ diametro.

Dioecious. Stem rather stout, up to c. 650 μ in diameter. Cortex irregular, mostly diplostichous but often partly triplostichous : cortical cells very long, with consequently very few nodes in a stem-internode : primary and secondary series usually of nearly equal size, the primary inclined to be slightly the broader. Lower portion of the stem ecorticate with usually the three uppermost internodes corticate. Spine-cells entirely rudimentary. Stipulodes in a single circle,

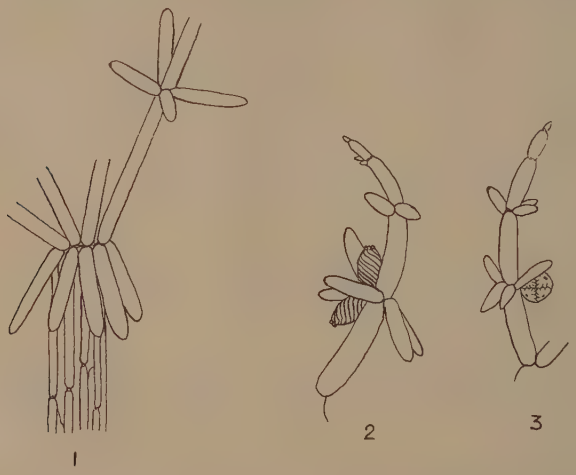

Fig. 1.—Stem-whorl, showing stipulodes and stem-cortex.
Fig. 2.—Female branchlet, showing position of geminate oogonia and downward pointing posterior bract-cells.
Fig. 3.—Male branchlet.
Magnifications. × c.5.

downwardly directed, decidedly unequal in length, equal in number to the branchlets, long, stout, with obtuse ends : often wanting (deciduous ?).

Whorls of 8–10 ecorticate branchlets which may be over 3 cm. in length : segments 4–5, inclined to be swollen, the terminal one short and conical. Bract-cells 3–4, often only two (occasionally 3 or 4) developed, produced mainly at the first and second nodes : somewhat swollen, obtuse, up to 2000 μ long but usually much shorter and often not more than one and a half times the diameter : c. 500 μ broad : some almost spherical in very young whorls : very irregular, especially in their direction, the posterior ones usually pointing downwards, which gives the plant an unusual look.

Oogonia may be solitary but frequently geminate, in which case one is directed upwards and the other downwards. Oogonium c. 1125 μ long inc. coronula, which is c. 250 μ broad and c. 125 μ tall, straight with short ovoid cells. Oospore dark reddish brown, c. 800 μ long and c. 450 μ broad, showing about ten striations. Antheridium c. 900-975 μ in diameter, produced at the first node only. Lime encrusted.

The figures are based on sketches by Groves, who first recognized this as a new species, though without specifying its special features beyond noting its affinity to *C. mollusca* Br. and *C. Hornemannii* Wallm. These are both haplostephanous species with a diplostichous stem-cortex and ecorticate branchlets. *C. Hornemannii* is however a very large plant with two stipulodes to each branchlet and conspicuous spine-cells whereas the present plant appears to grow in clumps about 15 cm. in height, has one stipulode to each branchlet and extremely small spine-cells.

It comes nearer to the Tasmanian *C. mollusca*, which also has one stipulode to each branchlet, but which is described (*Fragmente*, p. 116) as having sometimes an imperfect stem-cortex, very much smaller gametangia (oospore 400–500 μ long and 280–300 μ broad and antheridium 500–585 μ in diameter), the branchlet end-cell long and cylindrical and practically no lime encrustation; it also has more crowded whorls and is a more slender smaller plant.

Among the most striking features of the present species are the peculiar angles of the bract-cells, the situation of the geminate oospores and the very long stem-cortical cells.

It was originally collected on 1 August 1928 by Mr. E. R. Buckell in Sweets Lake, a small pond about five miles south of Vernon: and later in 1930, 1935, 1936 and 1938 from the same pond, a very restricted range. Careful collecting in this pond on 2 July 1946, produced no *C. Buckellii* but only *C. evoluta*.

The species is named after the late Dr. Edward Buckell. As type I designate the collections made by Mr. Buckell in 1930 (♀) and Oct. 1936 (♂) and these specimens are preserved in the British Museum (Natural History).

6. **Chara canescens** Lois. (*C. crinita* Wallr.)

Vernon (Sweets Lake), Aug. 1938: Savona, Aug. 1946.

Dioecious but only the female plant found: the male is only known to occur in a few places in the world and has not been recorded from the American continent. A very spinous plant, with spine-cells occurring on all the rows of the stem-cortex as no secondary cortical series is produced.

7. **Chara evoluta** Allen.

Vernon, Aug. 1935, July 1946: Shuswap Lake, Nov. 1935, Oct. 1936: Kamloops, Oct. 1937, July 1939: Lac du Bois, Kamloops, July 1940, July 1946, from seven small, shallow, range ponds.

A species very similar to *C. canescens* except for its being monoecious. Allen in 1882 described *C. evoluta* from a plant collected by Macoun in Saskatchewan.

8. **Chara contraria** Kütz.

Fairmont Hot Springs, Radium, July 1928, in very hot water: Wardle Creek, Kootenay National Park, July 1946, in very cold water: Keremeos, 1930: Penticton (Dog Lake), July 1931: Shuswap Lake, July, Aug. and Nov. 1935: Oct. 1938: Bridge Lake, July 1935: Pinantan Lake near Kamloops, June 1935: Lac du Bois Range, near Kamloops, July 1946, from two small ponds: Paul Lake near Kamloops, July 1946; (Paul Lake is 1·52 sq. miles in area and in places 150 ft. deep. *C. contraria* grows over the bottom from 10 ft. deep down to an unknown depth in a dense bed). Salmon Arm (White Lake), Aug. 1936; (Gardeners Lake), Oct. 1939: Clinton, July 1940: Lac la Hache, July 1940; Aug. 1946: Chilcotin District (Beaver Lake and Big Lake) July 1940: Fraser Lake, Aug. 1946; (Mr. Buckell records that this is the farthest north that he has seen *Chara* in British Columbia. Fraser Lake is a little north of latitude 54°.) Montana Lake, 1939: Mabel Lake, Aug. 1938.

Monoecious, stem-cortex two-ranked with the primary series more prominent than the secondary.

Evidently the prevailing species of *Chara*. The plants exhibit an extremely wide range of variation in detail. The commonest form has connivent branchlets, the Bridge Lake plant being the best developed. Among the smaller examples of this form, the Mabel Lake plant has a very irregular stem-cortex which in places is almost haplostichous and the very small spine-cells are sometimes geminate. The Beaver Lake plant, too, often exhibits little growth of a secondary cortex. The Shuswap Lake plant of Nov. 1935 has particularly well developed rather acute stipulodes, spine-cells, and bract-cells, and tends towards the var. *hispidula*.

Among the weaker forms there is much variety in the degree of branchlet cortication. In a Lac la Hache plant sterile whorls of entirely ecorticate branchlets occur, whereas in a Bridge Lake specimen there were some ecorticate branchlets bearing reproductive organs.

(It is perhaps worth noting that no specimens of the closely related *C. vulgaris* L., which has the secondary cortical series more prominent than the primary, were found in British Columbia, but Mr. Buckell collected this species (var. *longibracteata* Kütz.) in Alberta from Bow Lakes, Banff).

9. **Chara aspera** Willd.

Clinton, July 1940 : Lac de Bois Range, Kamloops, July 1946, from three small ponds.

Dioecious. Stem-cortex three-ranked, the primary series larger than the secondary. Spine-cells conspicuous, giving the stem a spinous appearance.

Several instances of bifid bracteoles and bract-cells noticed in the Lac du Bois plants.

The only previous Canadian record to my knowledge is Macoun's in 1879–1880 from Saskatchewan.

10. **Chara globularis** Thuill. var. **capillacea** (Thuill.) Zanev. (*C. fragilis* Desv.).

Dog Lake, Penticton, July 1931 : Vernon, Aug. 1928 : near Bridge Lake, Aug. 1935 : Shuswap Lake, Aug. and Nov. 1935, Oct. 1936 : Kamloops, July 1939 : Kinbasket Lake, July 1946 : Lac la Hache, Aug. 1946.

Monoecious. Stem-cortex three-ranked, the primary and secondary series about the same width : stipulodes and spine-cells rudimentary.

11. **Chara delicatula** Ag.

Shuswap Lake, Oct. 1932 : Lumby, Oct. 1936 : Three Valleys Lake, July 1937 : Mabel Lake, Aug. 1938 : Bridge Lake, July 1939.

Monoecious. Rather similar to the last species but the primary series of the stem-cortex is considerably larger than the secondary and the upper circle of stipulodes is developed to some extent.

The only other record of which I know is from Ontario.

PROCEEDINGS OF THE GENERAL MEETING ON 23 March 1950

Professor F. E. Fritsch, F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on Thursday, 9 March 1950, having been circulated, were taken as read and confirmed.

The president announced that it had been decided to award this year's Linnean Medal to Mr. H. N. Ridley, C.M.G., M.A., F.R.S., F.L.S.

The following were thanked for gifts made to the Library since the last Meeting : Mr. I. H. Burkill, Rear-Admiral Tufton P. H. Beamish, C.B., and Dr. H. T. Güssow.

In accordance with Chap. 10, Sect. 8 of the Bye-Laws, the following Fellows were elected, by show of hands, as Auditors of the Treasurer's Accounts for 1949–50 :—

Representing the Council :—Dr. H. W. Parker.
Dr. George Taylor.

Representing the Fellows :—Mr. I. H. Burkill.
Miss E. M. Wakefield.

The following Fellow signed the Obligation in the Roll and Charter Book and was admitted a Fellow :—Dr. E. Ashworth Underwood.

Certificates of recommendation for election to Fellowship of the Candidates named in the Agenda of the present General Meeting were taken as read for the second time.

Read for the first time certificates of recommendation of the following Candidates for ordinary Associateship :—Miss Joan Bain, B.Sc., Miss Ailsa McGown Clark, B.A., Frank Nigel Hepper, George W. Shaw, Denys William Tucker, B.Sc. and Alan Wesley, B.Sc., A.R.C.S.

The President reported the death of Dr. Robert Gurney, Fellow of the Society.

A Joint Discussion with the Systematics Association, on Biometrics and Systematics, was opened by Dr. R. Melville, Professor Duncan Leitch and Dr. C. B. Williams. (In his absence through illness, Dr. Williams's contribution was read by Dr. J. P. Harding.)

In the general discussion the following took part :—Dr. E. J. H. Corner, Mr. W. T. Stearn, Mr. P. C. F. Sylvester-Bradley, Dr. W. B. Turrill, Dr. J. Heslop Harrison, Dr. E. Trewavas, Dr. A. Tindell Hopwood, Dr. B. P. Uvarov, C.M.G., F.R.S., Dr. H. W. Parker; Dr. Melville, Prof. Leitch and Dr. Turrill replied.

A JOINT DISCUSSION WITH THE SYSTEMATICS ASSOCIATION, ON BIOMETRICS AND SYSTEMATICS

ON THE APPLICATION OF BIOMETRICAL METHODS IN PLANT TAXONOMY

By R. Melville.

(With 4 text-figures.)

Taxonomists generally have a dislike of mathematics and are loath to apply mathematical methods to the study of taxonomic problems. This dislike is reflected by the use in plant descriptions of qualitative terms such as smaller and larger, broader and narrower, which only in recent decades have been replaced by precise measurements with an indication of the range of variation. A distinct difference in mental outlook distinguishes the mathematician from the biologist. The mathematician delights in abstract theorizing and is prepared to overlook small details that may prevent the expression of his conclusions by a simple formula, whereas the biologist concentrates on the wealth of detail necessary for the characterization of species. Sometimes this attitude of the biologist crystallizes into a strong aversion to mathematics as evidenced by Huxley's *obiter dictum* quoted by D'Arcy Thompson[1] that 'Mathematics is that study which knows nothing of observation, nothing of experiment, nothing of induction

nothing of causation'. Again, Bergson[2] took the extreme view that, 'Calculation touches, at most, certain phenomena of organic destruction'. Few nowadays would subscribe to such perverted sentiments, so let us turn from the extremists and examine some of the applications of mathematics in plant studies.

One of the simplest applications is the determination of the average or mean of a series of measurements of some character such as the breadth or length of leaves or petals. An estimate of the variability of the sample is provided by the determination of the standard deviation or of the probable error. One may then judge whether the means of two groups differ significantly, or if it seems desirable, pass on to more elaborate statistical tests designed expressly to establish the significance or otherwise of the difference.

Although the mean values of a character, with the standard deviation, enable one to form a sounder opinion as to the distinctness of two groups or taxa, it is only by the combination of a number of preferably unrelated characters that their distinction as separate entities can be established. It is of much greater interest, therefore, to consider methods of distinguishing varieties and species which overlap so much in their morphology that it is often difficult to decide by simple examination in which group to place a particular specimen. One way of doing this is to combine a number of characters to produce a plant index. A simple method was worked out by Anderson and Whittaker[3] in a study of *Uvularia grandiflora* and *U. perfoliata*, two North American bellworts (Liliaceae). The two species are quite readily distinguished by several disjunctive characters so that at no time was the identity of any specimen in doubt. Furthermore, they possess a number of characters in common that overlap to such a degree that the allocation of many individuals is doubtful on these criteria alone.

U. grandiflora is a somewhat larger plant than *U. perfoliata* and has generally fewer nodes below the first branch on the stem and also has more nodes on the lowest sterile branch. These two characters were combined with three ratios calculated from measurement of the leaves.

As our appreciation of differences rests largely on the distinguishing of shapes and since a ratio can give a better estimate of shape than a simple measurement, we may expect to find less variation within the ratios than in the direct measurements. This proves to be so, and Anderson and Whittaker found much less overlap in the ratios than in the measurements. The ratios were then combined into a leaf index by taking the square root of the sum of their squares. The leaf indices still overlapped but to a lesser degree than the other criteria. When the two stem measurements were incorporated to form a general plant index the values of this index were disjunctive and could be used effectively for the determination of any individual.

Anderson and Whittaker explain the process graphically by illustrating the three leaf ratios as edges of a rectangular box meeting at one corner. The diagonal from this corner to the opposite corner of the box provides the leaf index. It may not be at once apparent to the non-mathematical, that this is only an extension of the theorem of Pythagoras, but this is obvious when only two characters are considered. The hypotenuse of the first triangle (Fig. 1) then forms one of the sides containing the right angle of the second triangle. The third character provides the length of the other side and the hypotenuse of the second triangle gives the index for the three characters. The process may be continued indefinitely until as many characters as desired have been incorporated in the index. This kind of index might well be called a 'Pythagorean Index'. Once the range of variation of the index for the two species has been determined any individual can be satisfactorily placed. Incidentally, this graphical method is an easy means of arriving at the square root of the sum of the squares of a set of observations, a figure that is often needed in statistical work. It has the beauty of simplicity and the only tools required are a ruler and a set square.

It seems probable that most species and varieties could be distinguished by the use of a Pythagorean index and, when this is so, it is unnecessary to go to any further mathematical elaboration. If, however, it is necessary to distinguish some small variant within a species, such as a particular clone of special economic value, then a still more critical method may be required. I may quote as an example the shipmast locust, a silvicultural form of the black locust, *Robinia pseud-acacia*. In his study of the problem Henry Hopp [4] found that this form differs from typical trees of the species by four bark characters none of which was sufficient to distinguish it. A further complication was that three of the bark characters vary with age and the diameter of the tree. A composite discriminant factor was found in a ' Bark Index ' obtained by weighting each character by a numerical factor according to its value for discriminating between the two forms and then adding together the weighted values of the characters. The bark index of any individual of this species can be calculated by substituting the appropriate measurements in the equation :—

$$\text{Bark index } Q = 0{\cdot}01572A + 0{\cdot}0185B + 0{\cdot}1161C - 0{\cdot}1597D - 0{\cdot}0096E.$$

The practical application of the method is simple enough, once the research worker has determined the values of the coefficients needed to weight each character. The solution of such a problem calls for a very critical examination of the

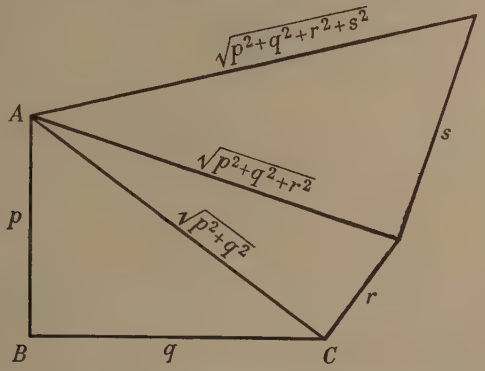

FIG. 1.—Derivation of a ' Plant Index ' from an application of the Theorem of Pythagoras. The theorem states $AC^2=AB^2+BC^2$. The hypotenuse can be regarded as a resultant of the two sides p and q representing by their lengths the magnitudes of measured characters of the plant. For a series of characters the Plant index $P=\sqrt{p^2+q^2+r^2+s^2+\ldots}$

basis on which the discriminatory value of a character depends. Three factors are involved :—

1. The degree of interrelation between the characters employed, which can be measured by correlation coefficients.
2. The magnitude of the difference between the two taxa, which can be expressed by the difference between their means.
3. The magnitude of the variation within each taxon, which is guaged by the standard deviation of the means.

The principles enunciated by Hopp are of general application, though details of the solution of his particular problem of the shipmast locust need not concern us here, they can be sought in the original paper.

A critical assessment of the value of individual characters was made on rather different lines by Anderson and Ownbey [5] in considering the differences between

Nicotiana alata and *N. langsdorfii*. It was found that in these two tobaccos a fairly constant proportional difference in cell size existed in all parts of the plant. *N. alata*, which had the larger cells, also had relatively more elongated cells and with this was associated a more acute angle of branching. Cell elongation and angles of branching were shown in an associated study by Nagel to be correlated with a greater production of growth hormones by *N. alata*. The different sizes and proportions of the cells in the two species affect all the plant organs to a greater or less extent, so that the question arises, where is it best to measure the differences? In these tobaccos, cell size was found to be least affected by extraneous factors in the corolla throat, and could be guaged by its diameter. Cell elongation, on the other hand, was best represented by the relative lengths of the corolla tubes. The angle of branching could be measured from the branches or by determining the angle between the lateral nerves and the midrib in the leaf.

From a consideration of the differences exhibited by *N. alata* and *N. langsdorfii* it seems probable that a small number of fundamental growth factors underlie many of the characters capable of measurement in plants. By measuring the length and breadth of leaves, calyx lobes and petals, for instance, we are in fact measuring only the same factors in slightly different combinations. Although

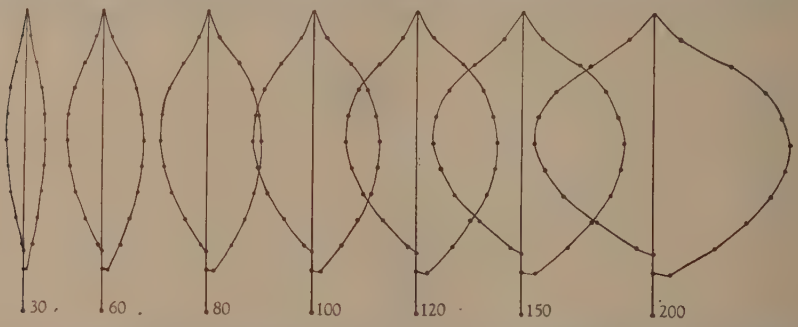

FIG. 2.—Arithmetic deformation. A series of leaf shapes, forming part of an arithmetical series obtained by calculation from the mean shape of the subdistal leaves of short shoots of an individual of *Ulmus carpinifolia* Gled., taken as 100. The leaf shapes within this species cover at least the range 60 to 150.

it is well to keep this possibility in mind when planning a biometrical research, in many studies we are limited by the material available. Where flowers are not available, or unsatisfactory on account of size or other considerations, as in my own studies of the elms, then equally appropriate criteria of specific distinctness may be obtained from leaves, or other organs. Even the further restriction of material in a fragmentary or comminuted state does not preclude specific discrimination. This is well exemplified by pharmacognostical studies employing cell measurements and such criteria as stomatal numbers, stomatal index and palisade ratios.

We may, accordingly, draw the conclusion that leaf shape characters have a valid foundation in the fundamental cytological and physiological differences between plants. Leaf shape is the resultant of the operation of a number of growth factors. It may, in fact, be regarded as a stress diagram of the forces that have combined to produce the shape. Since the principles involved in the comparison of leaf shapes apply equally to the shapes of other organs such as petals, sepals, bracts or fruits, it will be convenient to limit my remarks to leaf shape. On taking up the study of elms I was driven to examine the possibility of employing leaf shape for discriminating between the species. In the genus *Ulmus* the flowers are small and so simple that they provide few characters of any value. Similarly,

the fruits are flat samaras which scarcely differ from one another in many species. On the other hand there is such a welter of variation in leaf shape that it frequently led earlier systematists astray.

My attention was quickly focused on the most stable leaf types to be found on the tree, those of the short shoots situated on the normal branches of the crown of the tree. Leaves on suckers and epicormic shoots are of a juvenile type and in successive years pass gradually into the adult type. The leaves of proleptic or Lammas shoots show some juvenile features, but differ in shape from those of the short shoots. The long shoots or extension shoots also have features of their own and this does not exhaust the variation. As my purpose was to determine the average leaf shape characteristic of an individual or species, it may at first appear that the correct procedure would be to sample all these different types of leaf and so obtain a mean. Such a procedure would be unsound. It is absolutely essential in any biometrical work to confine comparisons strictly to organs of one class or grade. So far as leaves are concerned, valid comparisons can only be made between leaves taken from corresponding positions on a tree. Although it was found that the group of leaves occurring on a short shoot provided a leaf ' spectrum ', which is characteristic of the species, considerations of time and labour forced me to confine my attention to the distal and subdistal leaves. If only one leaf type can be dealt with, the subdistal leaf is the best one to choose in *Ulmus*. Other genera must needs be considered on their merits, although the same general principles will apply.

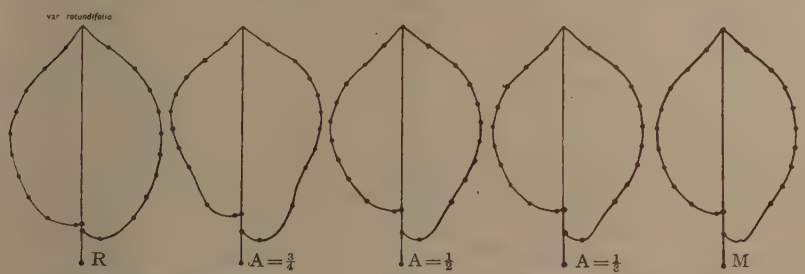

FIG. 3.—Logarithmic deformation. At the left is the mean leaf shape of subdistal leaves of the type of *Ulmus coritana* var. *rotundifolia* Melville. The three intermediate shapes were obtained by distorting the co-ordinate grid logarithmically from base to apex using the three factors shown. The shape at the right has been adjusted from that next to it to correspond in breadth with the mean of *U. coritana* var. *media* Melville, which it fits very closely. (For details see Melville, 1949.)

In some taxonomic problems, such as that in *Uvularia* already cited, it is sufficient to make a few simple measurements of length and breadth and the position of maximum breadth. Much greater use can be made of leaf shape if the entire shape is employed instead of a few abstractions from it. Several workers, for example Lindquist [6], have done this by grading leaves into size classes and then making measurements on squared paper, finally averaging the resulting figures to obtain a series of figures which, when plotted, give a mean leaf shape.

This is a simple and rather crude application of Cartesian co-ordinates. A much neater and more accurate technique [7] is to make tracings of the leaves and project these by means of a photographic enlarger of the automatic focusing type so that the image just fills a standard sized grid divided into tenths and hundredths. The midrib is arranged along the central line of the grid and the breadth of the leaf or half leaf at any desired interval can be read off directly in terms of a percentage of the length of the leaf blade. It is no longer necessary

to grade leaves into size groups, as leaves of any size can be used. It is possible also to take random samples of leaves from comparable positions. As the measurements are expressed in percentages, the figures can readily be averaged or submitted to a statistical analysis.

A set of Cartesian co-ordinates can be employed as a means of conveying a precise definition of any outline however complex. It takes but a short time to plot the data on squared paper and to transfer the outline on to Cellophane for comparison with other similar figures plotted on the same scale. In this way the magnitude of the differences between different individuals, species and other groups can be determined exactly and precisely located. Small fluctuations in the shapes are ironed out in the means and the attention is focused on the significant features of the shape that are of value in delimiting the group.

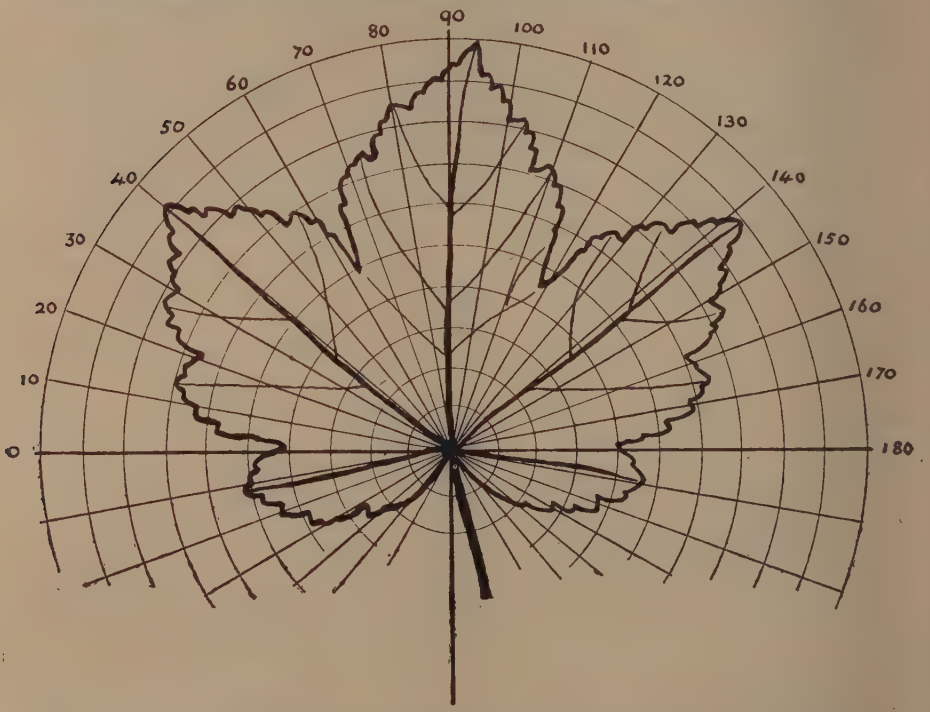

FIG. 4.—Outline of a leaf of *Acer pseudoplatanus* L. superimposed on a grid for the determination of polar co-ordinates. The base of the midrib is taken as the focus and its length as 100. Any point on the outline can be defined by an angle and its distance from the focus, which is expressed as a percentage of the length of the midrib.

Apart from their value in defining a shape precisely, the co-ordinates can be distorted in various ways by simple mathematical treatment. For example, it is a simple matter to derive a family of shapes in arithmetical proportion and compare these with the variation observed in nature within the limits of a species. Variation of this kind is not uncommon among elms and there is a strong tendency for it to be correlated with geographical distribution. The results may then be expressed as a topocline in leaf shape.

Not infrequently other variations of shape are superimposed on the simple arithmetic series. These may take the form of a relative elongation of the basal or apical region or perhaps a relative broadening of the basal region, while other

parts of the leaf remain comparatively unchanged. To say this, means of course that growth is relatively greater or more prolonged in those regions that enlarge more in the one species or individual than in the other. Often a logarithmic deformation of the one set of co-ordinates will give an outline closely fitting that of the other. When this is so, it may be regarded as evidence of relationship, provided that other independent characters support such an opinion. A certain amount of caution is necessary in interpreting the results of transformations as the shapes encountered throughout a genus are commonly related. Theoretically at least, any one of them could be transformed into any other by appropriate mathematical treatment.

Another field in which the co-ordinate method can be used is in the study of hybrids. The leaf shapes of putative parents can be combined in various proportions and the shapes obtained compared with those of the suspected hybrid. The leaf shapes of F_1 hybrids are commonly intermediate, but those of later generations or back crosses may exhibit various recombinations of the characters of the parents. Again, in the the study of hybrid swarms the co-ordinate treatment of leaf shape offers a means of classifying groups that defy more stereotyped methods.

Rectangular co-ordinates have proved to be a very useful tool in the critical study of elms, but polar co-ordinates could provide an alternative technique. With certain structures polar co-ordinates might lead to a simpler mathematical treatment than rectangular co-ordinates, for example, palmate leaves. Here a very definite node exists at the point of departure from the petiole of the principal nerves or leaflet midribs, which could be used as the focus or origin of the co-ordinate system. Pinnate leaves could, of course, be treated in similar manner using either the base or apex of the lamina or the point of attachment of the stem and petiole as the node. No one, I believe, has yet explored the potentialities of this technique in plant taxonomy.

In this brief review I have touched upon a few of the applications of biometrical methods in plant studies. No doubt there are other techniques as valuable as those I have mentioned. There is, undoubtedly, a very wide field of application for these techniques, of which no more than the fringe has yet been explored.

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BIOMETRICS AND SYSTEMATICS IN RELATION TO PALAEONTOLOGY

By Duncan Leitch.

(With 9 text-figures.)

During the past fifty years, certain problems in systematics have become apparent to the palaeontologist, many of which are distinct from those of the neontologist. These are largely concerned with (*a*) the nature of the material upon which diagnoses and classifications have to be based, (*b*) the speculative

nature of much of the evidence regarding the geographical and ecological conditions under which the organisms lived, and (*c*) the influence of the time concept on classification.

The palaeontologist has to rely on the evidence of a complex of morphological characters on which to differentiate his various types and in any attempt to arrive at ideas regarding either the systematic relationship or the evolutionary history of his groups, he has to reduce this complex to measurable units which can be analysed either amongst contemporary forms (at one horizon) or in successive stages (at various horizons). Moreover, his evidence is entirely confined to the hard parts and while he may arrive at some conclusions, through various indirect means, regarding the conditions under which the organisms lived, any views regarding the nature of these characters, whether adaptive or otherwise, must be for the most part speculative. It is therefore not surprising that in palaeontological work, the taxonomic categories are more arbitrary than is usual in neontology.

Moreover, the time concept and the idea of a fluid constantly evolving system necessitates the establishment of systematic groups which are more than morphological units. The palaeontologist has in fact to produce diagnoses which will express something of the evolutionary history and probable genetic relationships of the groups and yet satisfy the requirements of the stratigrapher who is primarily concerned with their recognition in the field and in the museum rather than with their ancestry.

In the main, attention has been concentrated on the latter requirements, and diagnoses have dealt mainly with the comparison of selected individual types. Consequently, little difficulty has been felt regarding nomenclatural procedure especially where only a few odd specimens were known and these at widely separated horizons; nevertheless problems did arise owing to the repeated occurrence of homeomorphs and to the need for some information regarding phylogenetic relationships. Recently, however, considerable work has been directed towards the study of evolving communities, rather than of individuals, and the resulting concept of slowly evolving anastomosing networks of descent which we call lineages, and which at successive horizons exhibit wide variation, has made it obvious that the simple two-dimensional pattern, which may be ample for the classification of living forms, must be replaced by one which is at least three-dimensional, and which must, in fact, if we accept continuity in evolutionary change, ultimately become multi-dimensional.

This is not the occasion for discussing the relative values of two approaches to classification, the one based on morphological comparison only, the other based largely on descent: if, however, descent has to play any part in our classification, it does emphasize the need for careful biometrical and statistical analysis of the variable characters involved in the changing populations and also the evolutionary processes expressed in the growth-changes that are exhibited by the individuals which comprise these populations. Furthermore, it emphasizes the need for some revision in our present system of nomenclature, or at least the development of techniques which will cope with the difficulties as they arise. It would seem that, at least in palaeontology, we must accept a much wider, less rigid concept of species than has hitherto been employed.

Variation in Fossil Communities.

The successful use by Trueman (Davies and Trueman, 1927) and other workers, for correlation purposes, of the Coal Measures non-marine lamellibranchs (*Carbonicola, Anthraconaia, Naiadites, Anthraconauta, Anthracosphaerium*), which for so long were considered useless as zonal fossils owing to the wide variation which they exhibit and to the alleged long-ranged character of their species, owes much to the application of biometrics and to certain modifications in nomenclatural procedure.

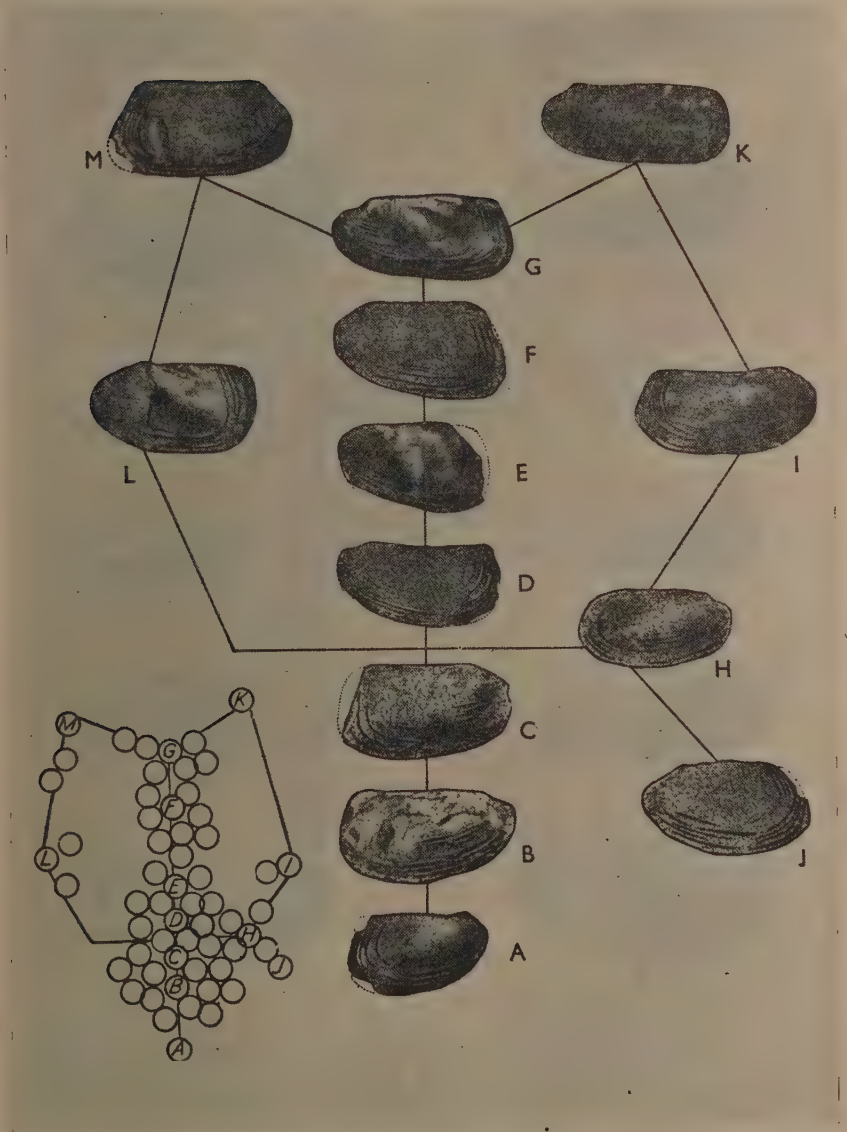

FIG. 1.—Variation intergrades of a community of *Anthraconaia* aff. *salteri* from above Musselband Coal, Lanarkshire, Scotland.
(By permission of the Geological Society of London.)

These shells occur in enormous numbers at various horizons in the British Coal Measures. At any single horizon, collections can be made from within a few inches of thickness of deposit which exhibit wide variation in almost every feature, including shell proportions, the character of the hinge and the general shell shape; moreover, these variations, when studied statistically can be shown in most cases to be continuous, one type grading imperceptibly to another. Such

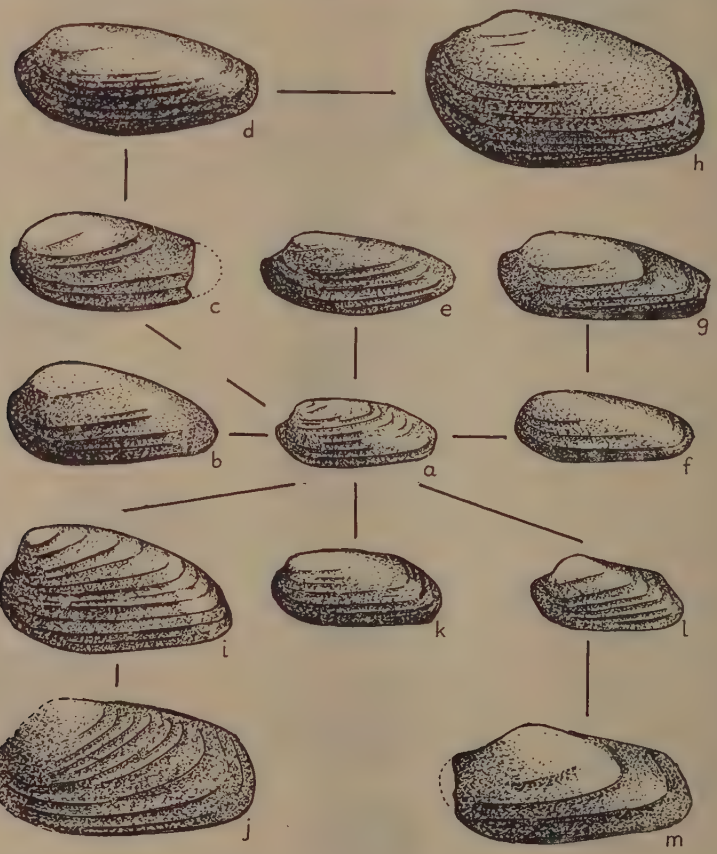

FIG. 2.—Diagram illustrating some of the more important species and variants within the *Anthracosia aquilina* species-group. (a) *A. aquilina* (J. de C. Sow.); (b) *A.* aff. *aquilina* (J. de C. Sow.); (c) *A.* aff. *aquilina* (J. de C. Sow.); (d) *A. atra* (Trueman); (e) *A. planitumida* (Trueman); (f) *A. acutella* (Wright); (g) *A. lateralis* (Brown); (h) *A. fulva* (Davies and Trueman); (i) *A. retrotracta* (Wright); (k) *A. concinna* (Wright); (l) *A. nitida* (Davies and Trueman); (m) *A.* aff. *aquilina* (J. de C. Sow.). Scale: reduced. (By permission of the Yorkshire Geological Society.)

homogeneous and indivisible communities may fairly be considered to have been contemporaneous and to constitute a part of a single Linnaean species. In fig. 1 some indication is given of the amount of variability which may be found within such a community (see also Leitch, 1936, 1940, 1942, 1947; Eagar, 1947). Such variation is, of course, not unusual in living forms and may present little difficulty to the neontologist. It does however present much greater difficulty to

the palaeontologist since he is concerned not with single faunas, but with many faunas from a number of successive time planes in which the derivative populations exhibit variation which may be comparable but by no means identical. Moreover, he is dependent upon these variable characters by which to differentiate these successive faunas and this differentiation is essential if they are to have any stratigraphical value.

Despite these difficulties however, it has been possible to develop a zonal scheme, the systematics of which have been intelligible to workers in the various coalfields and much of the success of which has been due to the application of biometric methods and to a special nomenclatural procedure which is briefly summarized below.

Where possible, communities and not single individuals were examined, especially in the earlier stages of the investigations. Such shell characters as the maximum length, height and width, the length of the anterior end, and various other characters were measured and statistically analysed. As the result of this analysis a number of species-groups were established, several of which extended

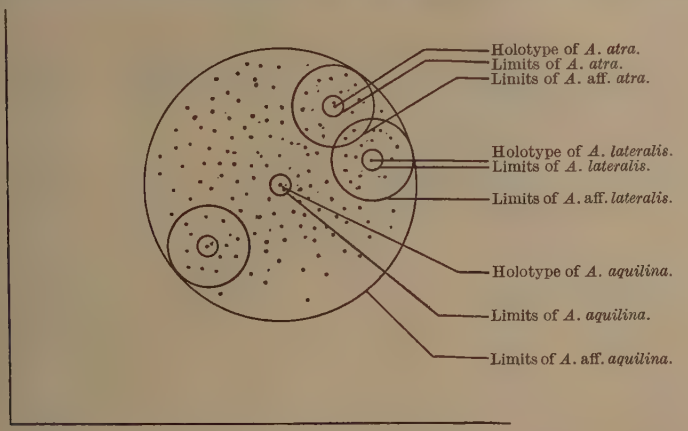
Holotype of *A. atra.*
Limits of *A. atra.*
Limits of *A.* aff. *atra.*
Holotype of *A. lateralis.*
Limits of *A. lateralis.*
Limits of *A.* aff. *lateralis.*
Holotype of *A. aquilina.*
Limits of *A. aquilina.*
Limits of *A.* aff. *aquilina.*

FIG. 3.—Diagrammatic representation of a cross-section of a species-group (for example, *Anthracosia aquilina*) showing the mutual relationships of some of the variants and morphological species within the group, and the procedure followed in their determination. For diagrammatic purposes only two directions of measurement have been shown.

through large thicknesses of the Coal Measures and which were regarded as continuously related in space and time. Particular attention was paid to the amount of variation which could be accepted within the scope of the species-group and the nature of any changes in variation at successive horizons. Where certain extreme variants were confined to particular horizons or at least were characteristic of a horizon or group of horizons, they were given separate specific rank. It thus happens that in some cases a whole species-group covering a multitude of variations in space and time may be designated by one specific name, while in others the group may be sub-divided into a number of selected types, each of which may be given a separate specific name. Fig. 2 illustrates, for example, some of the selected types which occur within the *Anthracosia aquilina* species-group.

In the diagnoses either of the species-group or of the related 'species', the normal practice was followed. Types were described in the usual way and the specific name was limited to forms practically identical with those chosen types. In order to deal, however, with the variants which lay in the transitional zones

either around the types of the species-group or between the types of the 'satellite' species, the use of the prefix *aff.* was emphasized. Let us, for example, consider the procedure in naming a member of the *Anthracosia aquilina* species group (fig. 3). Forms which are almost identical with the figured types would be designated *Anthracosia aquilina*: all other variants which are associated with these types or are believed to be within the scope of variation of the species-group would be referred to as *Anthracosia* aff. *aquilina*. A specimen determined as

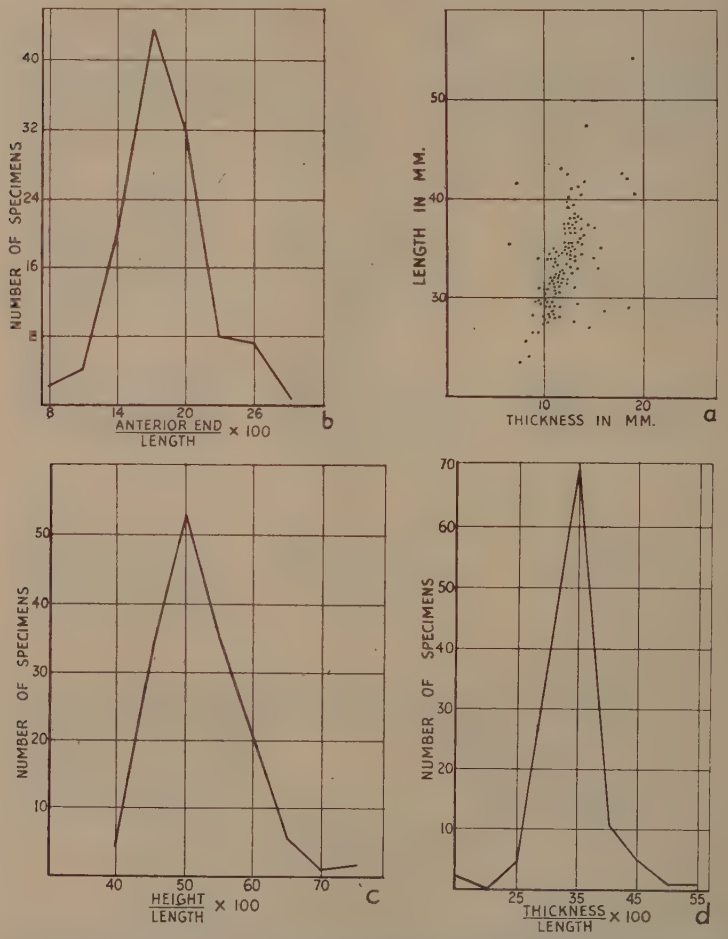

FIG. 4.—Variation scatters and frequency polygons of a community of *Anthracosia* aff. *atra* from above the Wathwood Seam, Wath-on-Dearne, Yorkshire.
(By permission of the Yorkshire Geological Society.)

Anthracosia aff. *aquilina* may nevertheless be as identical with, or within the variation surrounding one of the variant types to which specific rank has been given, for example, *Anthracosia atra*; in the former case the specimen would be determined as *Anthracosia atra* and in the latter it would be referred to as *Anthracosia* aff. *atra*. Consequently there may be considerable overlap in the naming of specimens, and one individual may, with equal correctness, be

determined as having affinity with shells which have been designated by more than one specific name. It will be obvious that when two or more names are used in this way they are not being used in the Linnaean sense.

In order to express the relationships and the ranges of the several variable characters, variation curves and scatters, coefficients of variation and other statistical values were calculated (figs. 4 and 5). It must be emphasized, however, that much of this work was done as a preliminary to the proper understanding of the full diagnoses; in subsequent determinations of individual specimens (for example in bore hole records from which only isolated specimens may be available) it is usually possible to do so largely by normal comparative methods.

In 1936, the writer expressed the opinion that while statistical analyses of separate characters showed the range in these separate characters, they failed to give any composite picture of the combined variational changes. He developed

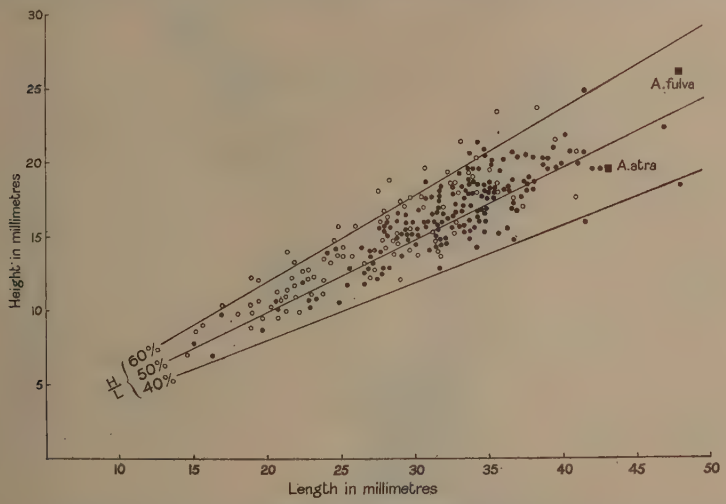

FIG. 5.—Variation scatter of the shells of a community of *Anthracosia* aff. *atra* (black circles) from above the Wathwood Seam, showing the relationship of the community to several earlier assemblages of the *A. aquilina* group (white circles) and to the types of *A. atra* and *A. fulva*.

(By permission of the Yorkshire Geological Society.)

therefore a series of pictographs in which selected intergrades were superimposed on a directional scatter and the remaining transitional members of the community were expressed as symbols in their respective positions within this composite scatter (fig. 1, inset). In this way, not only was the general variation pattern of the community shown, but also the nature of the predominant variant types. Eagar (1947) developed this method in greater detail and by superimposing pictographs at successive time planes has shown something of the evolutionary changes which have taken place in derivative communites (Fig. 6).

The above pictographic method was based largely on general impressions of shell shape and the results must not be regarded as an exact biometric analysis. In a further attempt, therefore, to make a precise differentiation of communties in which some of the variants were similar and yet the character of the variation of the communities was distinct, the writer (1940) proposed the use of multiple correlations and regression formulae, claiming that by such formulae any

significant difference* could be indicated mathematically. Moreover, it was pointed out that one could thus set precise limits to the variational character of an assemblage. The methods of using such formulae are summarized in fig. 7 and fig. 8.

The Establishment of Lineages.

In the foregoing we have discussed mainly the treatment of communities and the methods of determination of the variants which comprise them : we have discussed the assembling, where possible, of the several associated variants, into species-groups which we believe to have been related in space and time. Farther than that we cannot go ; the changing lithological (and presumably ecological) conditions from non-marine through marine to those of coal formation have resulted in a discontinuity of sequence which prevents us from claiming these

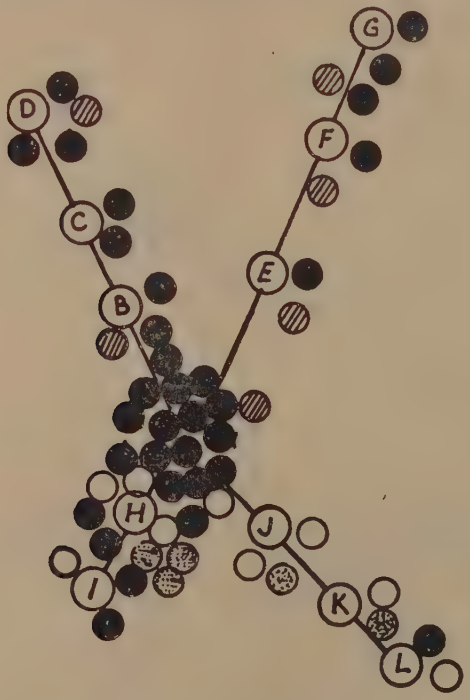

Fig. 6.—Distribution scatter of variants of *Naiadites tumida* at various horizons in the Limestone Coal Group of Scotland. The lettered circles represent figured intergrades. Other circles represent individual shells, their position in the framework being controlled by the resemblance to one or other of the intergrades. The various horizons are indicated by different symbols.

species-groups as true lineages. Other fossil groups, however, can be analysed in continuous sequences, under unvarying conditions and it is to these that we must turn for proof of descent and for the establishment of true lineages.

* If an *observed* value in any sample individual differs from the *calculated* value by more than twice the standard error, the individual is considered to be significantly different from the analysed community.

In palaeontology, just as the term species has increased in content, so also has the term lineage. The concept of a line of descent has given place to a broad plexus of evolving communites which may exhibit a wide range of forms at successive time planes, and the evolution of which can be expressed as a shifting mode of variation.

This idea and the place which biometrics has taken in its elucidation, is most simply exemplified in the work of Trueman (1922, 1924, 1930, 1940), Swinnerton (1940, 1941) and other workers on the Liassic oysters; these provide perhaps the most complete example of the palaeontological concept of lineage, for the successive homogeneous communities can be collected in large numbers in an

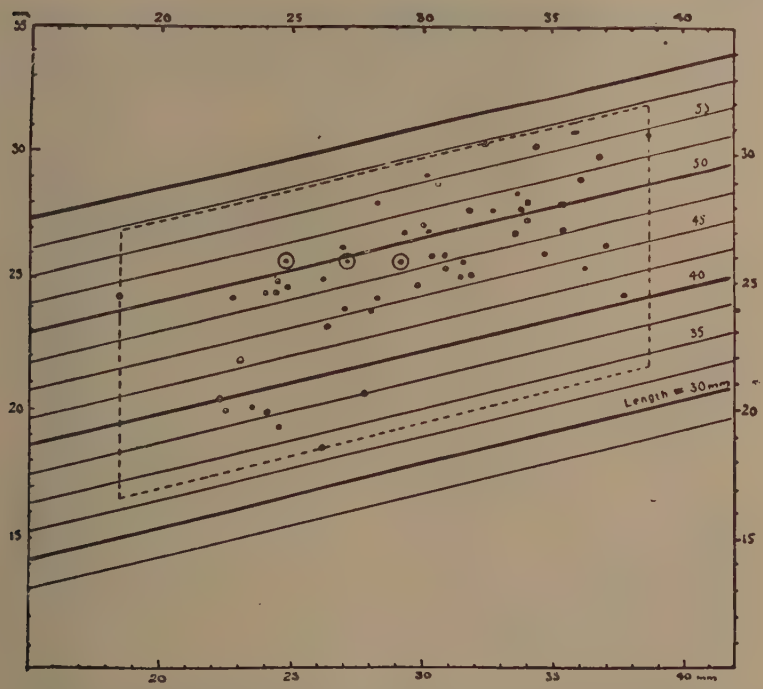

FIG. 7.—Graphical representation of the *Anthraconaia* aff. *salteri* community expressing three variables, length (l), height (h) and the position of maximum downward bulge of the ventral margin (d), based on the regression formula

$$h=0{\cdot}44l+0{\cdot}25d-2.8 \text{ (in mm.)}.$$

Three specimens have been encircled to indicate that the calculated heights (the abscissae) do differ from the observed height by more than twice the standard error ; that is to say they are significantly different.

The dotted lines indicate the maxima and minima of the three variables.

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almost unbroken stratigraphical sequence through a considerable thickness of strata and across a broad lateral extent at each time plane, and the resulting graphical representation of these communities leaves little room for doubt that we are dealing with a continuously evolving gens or lineage. This work has been amply discussed in several publications and so only a brief summary of the points relevant to this discussion need be given.

At various periods in the Mesozoic, oyster-like forms have become progressively modified into forms known as *Gryphaea*. The changes involved, most of which are measurable, have been summarized by Trueman (1922) thus :—

(1) Increase in coiling of the left valve, the early forms being flat while the later forms may be coiled through as much as one and a half whorls. This increase in coiling has also been expressed as a change in the spiral angle from 0° to 80°.

(2) Progressive reduction in the area of attachment.

(3) Increase in size.

(4) Progressive thickening of the left valve.

In a further analysis, Swinnerton (1940) has dealt with such variable characters as :

(1) The angle of the umbonal profile.

(2) The relative width of the shell.

(3) The tilt of the umbonal area with respect to the long axis of the shell.

(4) The slope of the umbonal area with respect to the shell profile.

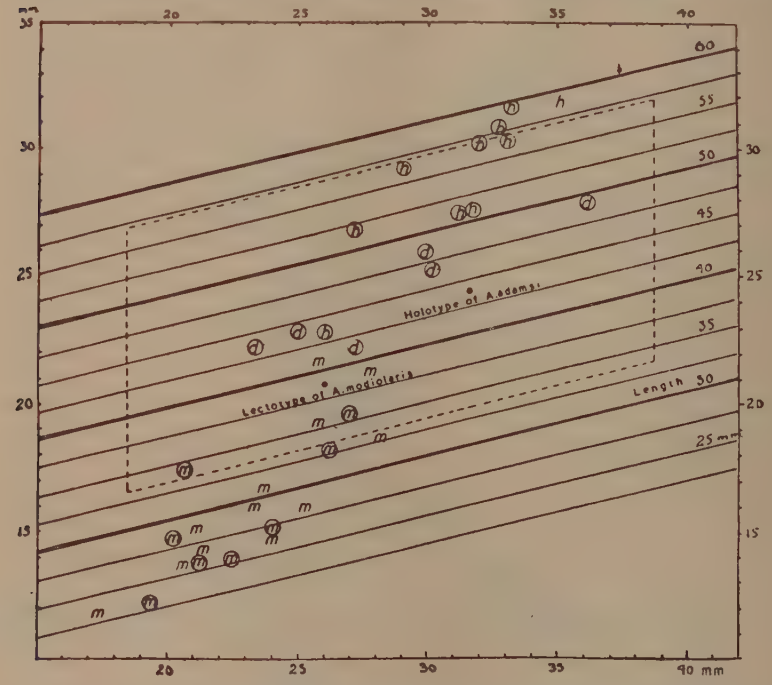

FIG. 8.—For comparative purposes, several variants of four species, *A. modiolaris* (m), *A. hindi* (h), *A. dolobrata* (d) *and A. adamsi* (a), all of which are closely comparable with variants of the *salteri*-community, have been superimposed on the *salteri*-scatter (fig. 7).

Note that the majority of these (encircled) are significantly different from *A. salteri*. (By permission of the Geological Society of London.)

The result of these investigations has been to show that at various periods the main oyster stock has deviated along definite lines which show progressive changes in the characters enumerated above, and it has been possible to establish lineages, the best known of which is *Ostraea irregularis—Gryphaea incurva* from the Lower Lias. This lineage forms almost a continuous series which can be linked from the flat oysters to the completely curved Gryphaeas. At each

horizon there is a wide range in the above characters, the change being almost imperceptible and only becoming obvious by statistical methods. In fig. 9 the increase in coiling has been graphed in relation to the number of individuals measured and the successive horizons have been marked by symbols : it will be noted that there is wide variation at each horizon, that there is considerable overlap at successive horizons, and that the evolutionary change within the lineage is marked by a shift in the mode of variation. In the 1922 paper (Trueman), apart from the emphasis which was placed on the variant types, and on the need for determination as communities rather than as individuals, little alteration was suggested in nomenclatural procedure, selected individuals (the modal forms at successive horizons (see fig. 9)) being chosen to represent the various stages in the lineage, but there is little doubt that it was from this work and perhaps more especially from the paper which followed (Trueman, 1923) that the wider concept of species, which has been discussed in earlier pages, received its greatest impetus.

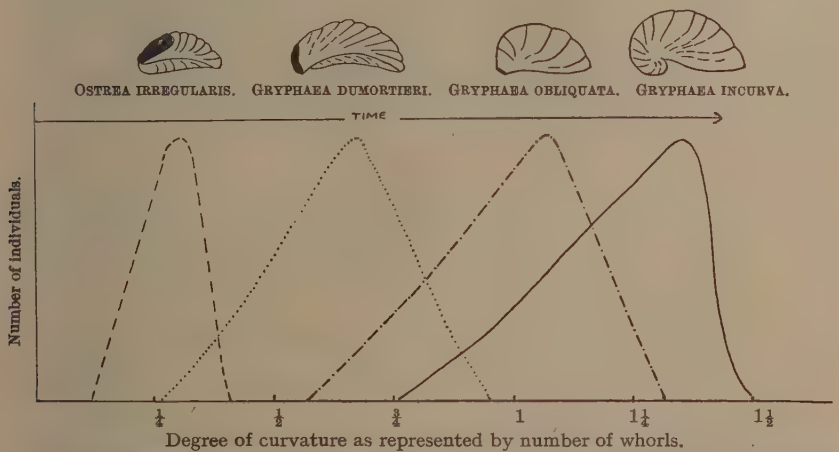

FIG. 9.—Frequency curves showing the range of variation in four successive communities (indicated by different symbols) of the *G. incurva* lineage. Above, the selected modal types to which specific names have been given and which illustrate increase in coiling and decrease in the attachment area (black) are shown.

Yet another requisite in the establishment of lineages and in the systematics of evolving communities is the analysis of individual growth-stages. If statistics prove that the stages passed through in a series of evolving communities are reflected in the growth of the individuals which comprise these communities, then it can be taken as further proof of consanguinity. Thus, for example, by careful measurements in the individuals of the characters involved in the evolution of the *G. incurva* communities, it can be shown that the phylogenetic stages illustrated in fig. 9 are represented at various ontogenetic stages in the individuals in the stratigraphical sequence : these results have been summarized by George (1933) as follows :—

Length of area of attachment as a percentage of the length of shell	Stage of growth as a percentage of the length of the adult shell in			
	Ostraea irregularis	*Gryphaea dumortieri*	*Gryhpaea obliquata*	*Gryphaea incurva*
90% (=*Ostraea liassica*)	60	33	11	5
50% (=*Ostraea irregularis*)	100	60	20	8
30% (=*Gryphaea dumortieri*)	—	100	33	13
10% (=*Grypheaa obliquata*)	—	—	100	40
4% (=*Gryphaea incurva*)	—	—	—	100

Thus "*G. incurva*, when it is one-twenty-fifth grown, is in the stage of *G. obliquata* one-tenth grown, or *G. dumortieri* one-third grown, or of an *O. irregularis* three-fifths grown, or of an adult *O. liassica*."

Conclusion.

In the time available it has been possible to quote only a few of the attempts to apply mathematical methods in the discrimination of morphology and in the better understanding of the evolutionary history of fossil groups. For the purposes of this discussion, emphasis has been placed on the Coal Measure lamellibranchs and the Liassic oysters but it must be noted that similar principles have been applied to comparable problems in the Foraminifera (Wood 1946), the corals (Carruthers, 1910) and the echinoids (Rowe, 1899). Much work has been done, more especially with a view to illuminating the nature of evolutionary processes in problems of relative growth (Huxley, 1932) and in the expression of some of the results in graphical form (Swinnerton, 1921), and there is little doubt that the results of such investigations will have their effect on the systematic treatment of fossils. Future investigations must also involve the relationship of these organisms to the lithology of the deposits in which they lived and were preserved. Eagar's work (1947, 1948) on the relation of shell-shape in lamellibranchs to the grain size of the sediments holds promise of interesting results.

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A NOTE ON THE RELATIVE SIZES OF GENERA IN THE CLASSIFICATION OF ANIMALS AND PLANTS

By C. B. Williams (Rothamsted Experimental Station).

(With 2 text-figures.)

For nearly two hundred years taxonomists have been classifying the animals and plants of the world by means of a system based on gradually differing degrees of relationships known as species, genera, families, and so on.

Each believes that by this system he is interpreting something real in nature, but he usually has insufficient evidence, and often has to base his conclusions largely on convenience, instead of what he considers to be more fundamental differences.

However, as a result of the work of thousands of systematists, we have classifications in various stages of completeness for nearly all groups of animals and plants, and the time has come when we may ask if there is any general principle running through these results, which might throw light on the fundamental natural relationships that they attempt to interpret.

One general principle, of a mathematical nature, has several times been pointed out and discussed. In almost every classification the number of genera with one species is greater than that with two, the number with two greater than with three, and so on; so that if we plot the classification in the form of a frequency curve, we get a 'hollow curve' somewhat resembling a hyperbola.

For example in Bentham and Hooker's 'British Flora' (1912 edition) there are 1252 species classified into 479 genera as follows :—

256	genera	have	1	species	each
84	,,	,,	2	,,	,,
51	,,	,,	3	,,	,,
22	,,	,,	4	,,	,,
21	,,	,,	5	,,	,,
8	,,	,,	6	,,	,,
5	,,	,,	7	,,	,,
5	,,	,,	8	,,	,,
5	,,	,,	9	,,	,,
6	,,	,,	10	,,	,, and so on.

If these frequencies are arranged in a diagram (Fig. 1) we get a 'hollow curve' somewhat like a hyperbola.

Many other examples could be given, from both animals and from plants; from world floras and faunas, and from those of quite small areas; but they all have the same general form.

Dr. J. C. Willis made considerable use of this in his 'Age and Area' theory, but both he and Chamberlin in the U.S.A. considered that the distribution was a hyperbolic or harmonic series. This was a mathematical error, as no finite number of species or genera can ever be arranged in a hyperbolic series. This series is divergent, and the sum of $1 . \frac{1}{2} . \frac{1}{3} . \frac{1}{4}$ etc. is infinite.

For the moment however it is not so much what particular mathematical formula will best represent the series, as the fact that there is always such a series, which is of interest. Is this mathematical order a figment of the taxonomist's imagination, or does it represent something real in the whole order of nature which he is trying to penetrate?

Since systematists with different ideas, in different groups of animals and plants, in classification based on quite different characters, practically all come to the same sort of curve, we may believe that it really represents some form of order in their classifications, and since order cannot be produced out of chaos

simply by taking a sample, then there must be some corresponding order in the natural relations of species and genera.

The ' hyperbolic ' series which was originally considered, in error, to be the explanation of the curve, is as follows :

$$n.\quad n/2\quad n/3\quad n/4\quad n/5 \ldots\ldots \text{etc.}$$

Where n is the number of genera with one species and the following terms those with 2 . 4 . etc. species.

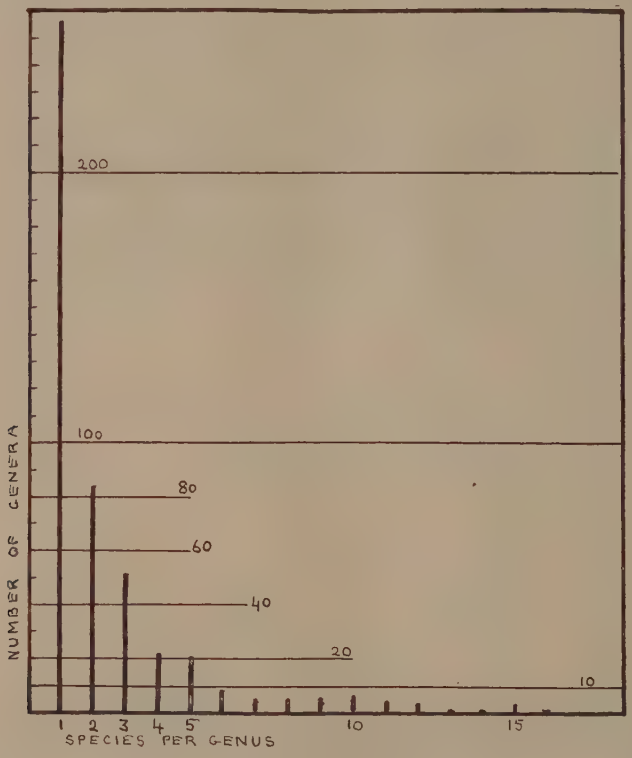

FIG. 1.—Frequency distribution of number of genera with 1 ; 2 ; 3 ; 4 etc. species in the British Flowering plants according to the classification of Bentham and Hooker (1912 edition) with 1251 species in 479 genera.

It was suggested by R. A. Fisher in 1943, in the somewhat similar problem of the grouping of individuals into species, that a possibly more suitable formula might be the logarithmic series, which can be written

$$x ;\quad \alpha x^2/2 ;\quad \alpha x^3/3 ;\quad \alpha x^4/4 ; \ldots\ldots \text{etc.},$$

where αx is the number of genera with one species : ' α ' is known as the ' Index of Diversity ' and is a property of the population sampled ; ' x ' is property of the sample, and is always less than one.

This logarithmic series has a finite sum both for the number of genera and the number of species. As it has two ' unknowns ', α and x, if we know the total number of genera and the total number of species we can calculate α and x, and so the whole series. In other words for a given number of species classified

into a given number of genera on the basis of a logarithmic series only one series is possible.

Thus in the classification by Kirby of 805 species of Mantidae classified into 209 genera, if this were a log. series, then α must be 91·6 and $x=0{\cdot}8978$.

Here the number of genera as calculated and as observed by Kirby is as follows :—

Number of species in genus	Number of Genera	
	calculated on log. series	observed by Kirby
1	82·3	82
2	36·9	28
3	22·1	27
4	14·9	12
5	10·7	20
1–5	166·9	169
5–10	26·0	24
11–20	12·8	13
21–50	3·0	2

It will be seen how very close the figures based on the log. series are to those recorded by Kirby. One might be inclined on this account to say that the ' logarithmic series ' is a correct interpretation of the structure of the genera–species relationship, and that Kirby gave an accurate interpretation of this structure in the Mantidae. I am inclined to agree that we may conclude that Kirby's classification was ' sound '—or perhaps better ' consistent '—but it is doubtful if we can say that it was ' correct '. This point requires further discussion.

Let us turn to the vexed question of ' splitter ' and ' lumper '. One authority asks for great differences before he separates a group of species into two genera ; another only requires the slightest excuse. Had Kirby been a generic splitter he might have classified his 800 odd species into 400 genera instead of 200 : if a ' lumper ' he might have been content with only one hundred genera. For each it is possible to calculate logarithmic series as follows :—

log. series for 800 species in 400 genera.
144 : 52 : 25 : 13·5 : 7·75 etc.

log. series for 800 species in 100 genera.
29 : 14 : 9 : 6·5 : 5 etc.

And I believe that in each, if Kirby had been equally consistent in the application of his principles, his classification would have conformed to one or other of these series, according to whether we imagine him as a ' lumper ' or a ' splitter '. In other words both classifications might have been ' sound '.

What then are we to conclude about right or wrong in classification ?

My own opinion used to be that *species* as used by taxonomists were about 90% real biological entities and about 10% matters of convenience or personal idiosyncrasy : *genera*, on the contrary, I considered to be about 10% real and 90% imagination. When however it was found that the same mathematical law seemed to fit the grouping of individuals into species, and the grouping of species into genera, I began to consider that ' genera ' might be as real as ' species '.

But when we see that there can be one series for the ' lumper ', one for the man of moderate opinion, and still another for the ' splitter ' we begin to doubt both genera and species.

There is however another possibility.

It is conceivable that—each in its own way—the different classifications of the lumper and the splitter represent equally truthfully what has happened in Nature.

It is not possible at present to support such a contention by direct evidence, but I will endeavour to show that it is not impossible theoretically.

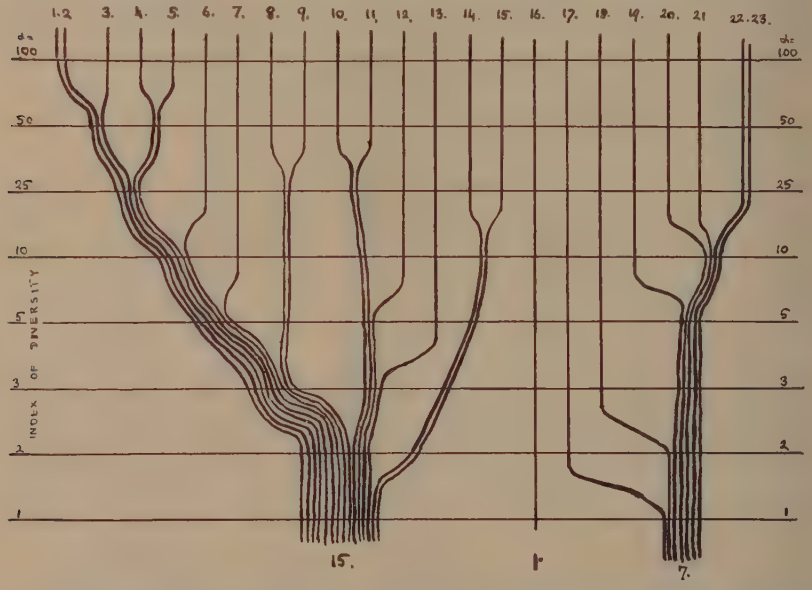

FIG. 2.—Imaginary genealogy of twenty-three species, showing the possibility of different levels of generic grouping, each of which is a correct interpretation of the relationships. Each gives a close approximation to a logarithmic series in the frequency distribution of genera with different numbers of species.

In Fig. 2, I have drawn an imaginary history in time of twenty-three species of some group. They have branched off in the past from the common stock and from each other, as we all believe species to have branched off.

If a splitter takes the 23 species and is prepared to accept as generic difference any separation which has occurred within comparatively recent times, he will classify the group into 19 species each in its own genus and two genera each with two species (top transverse line). This is a close approximation to a logarithmic series with $\alpha=100$ (see Table I).

TABLE I.—Twenty-three species divided into different numbers of genera, each arrangement approximating to a logarithmic series.

No. of genera	Index of diversity	Number of genera with—species 1	2	3	4	5	6	7	9	13	15
21	100	19	2	–							
19	50	16	2	1							
16	25	12	3	–	–	1					
12	10	7	3	–	1	–	1				
9	5	4	2	1	–	1	–	1			
7	3	3	1	–	1	1	–	–	1		
5	2	2	1	–	–	–	1	–	–	1	
3	1	1	–	–	–	–	–	1	–	–	1

If a man who is less of a splitter probes more deeply into the past he will find (second transverse line) evidence of one genus with 3 species, two with 2 and 16 with one. This is also a logarithmic series with $\alpha=50$.

Similarly if we require greater and greater differences before we will allow separate genera, we can find log. series at various levels till we reach the lowest, the outlook of the extreme ' lumper ', with only 3 genera for the 23 species ; one with 1 species, one with 7, and one with 15. This is also a close approximation to a logarithmic series with an Index of Diversity of 1.

I do not want to press too seriously either a purely hypothetical pedigree, or the suggestion that the logarithmic series is the one and only series that should be considered ; but it does seem possible that any of the half dozen alternative classifications of a group of species with such a pedigree would be equally correct.

Kipling has said :

" There are nine and sixty ways, of constructing tribal lays,
And every single one of them is right ".

Perhaps the same is true of systems of classifications of individuals into species, species into genera and so on.

If this interpretation is acceptable we find that the *relative* relationships that we call species, genera, etc, are real—but the point at which we draw the line is a question of personal opinion. There are of course bad systematists ; those who misinterpret characters, or are inconsistent in the application of their ideas ; but two or more good systematists who are consistent in the application of their principles may come to different conclusions, all of which may be equally correct.

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GENERAL DISCUSSION

Mr. Sylvester-Bradley commented on the difficulty of reconciling the species concept of the neontologist with that of the palaeontologist. The American palaeontologist Burma has gone so far as to declare that ' a species . . . . is a fiction, a mental construct without objective existence.' (Burma, 1949, Evolution, *3*, p. 369). However, to deny the reality of species, on the grounds that all are derived by gradual stages from a common ancestor, is as absurd as to deny the separate existence of twigs on a tree since all have sprung from a common trunk. The problem in neontology is to distinguish twig from twig. The palaeontologist not only has to discriminate twig from twig and branch from branch—a process in which the species has the same significance as in neontology ; he also has to distinguish the older part of a branch from a younger part. The neontologist has to deal with discontinuities which are the result of the process of a split in the phyletic line (the ' cladogenesis ' of Rensch). The palaeontologist also has to consider continuous change within a single phyletic line (' anagenesis '). It seems essential in this case to define arbitrarily the limits of chronological species on the basis of quantitative morphological change. Burma (1948, J. Paleont. *22*, p. 731) has suggested that the range of the species could be defined by the expression $M \pm 3\sqrt{2\sigma_M^2}$. To define the species in terms of the standard error would, however, clearly be subjective,

for, as $\sigma_M = \frac{\sigma}{\sqrt{N}}$, the range of the species would then vary according to the size of the sample. A more satisfactory criterion would perhaps be that suggested by Haldane (1949, Evolution, *3*, p 52) when he comments that, on the basis of a metrical character alone, ' if two fossils differ by more than about four times their standard deviation, they would be regarded as almost certainly derived from different species '. The standard deviation is at least an intrinsic character of the population, but its use as a ' yard-stick ' is open to certain other objections.

Dr. W. B. Turrill emphasized the need for great care in regard to the material examined statistically and the characters selected for statistical analysis. Biologically there is the double danger of ' not playing fair ' : (*a*) in not having random samples and (*b*) in scoring unsuitable characters. Sometimes, perhaps often, herbarium collections are not random samples in the statistical sense but include a high proportion of unusual deviations from the mean. Again, in, for example, leaf measurements of herbs, it is often difficult to fix objectively the actual leaves to be measured, at least in any way comparable to the fixing Dr. Melville has done for the side-shoots in elms.

Dr. J. Heslop Harrison : I should like to endorse the comments of Dr. Turrill in connection with the choice of characters for biometrical study in dealing with taxonomic problems in flowering plants. It is evident that biometrical methods are likely to be of most value to systematists in groups in which overlapping variation makes the delimitation of species or subspecies a matter of difficulty, and in which such morphological differences as do exist are quantitative and probably controlled by polygenic systems. Such a situation exists, for example, in the dactylorchids, where extreme intrinsic variability of populations is accompanied by geographical variation of population means, and where the taxonomy is further complicated by the occurrence in nature of hybrid swarms. It is commonplace that in such groups as this, not all of the criteria which have been employed in classical description prove to be of equal value when populations rather than individuals are made the object of study. To be of use in critical comparison, the familiar descriptive clichés of species diagnoses require more precise definition in terms of population parameters. The practical problems to be solved in accomplishing this may be considerable. As Dr. Turrill has pointed out, valid results can be obtained only by the random sampling of wild populations, since herbarium material is rarely sufficiently representative. In a large scale survey, economy of effort demands that the optimum sample size be known in advance, and that the characters which are measured or otherwise assessed in such samples should be such as to give maximum indication of the genetical structure of the populations ; that is, they should be those which are least susceptible to environmental modification. In groups in which cultivation difficulties preclude analysis of cultures in controlled environments, pilot studies of isolated, medium sized natural communities can often provide useful information. It is initially necessary to assume that a population so chosen represents a single taxonomic unit, and is, in cross-fertilized species, panmictic. The validity of such assumptions can usually be checked from the results obtained. From a pilot study of a natural population in an ecologically uniform habitat a rough assessment of the relative value of the characters considered of taxonomic significance can be obtained from a comparison of their coefficients of variation. Comparable statistics from a similar analysis of a population from an ecologically diverse habitat can then be used to reveal which of the selected phenotypic characters show least increase of variance and which therefore provide the most reliable indication of genetical structure.

We have heard from Dr. Melville something of Anderson's method of treating hybrid populations by the computation of an aggregate 'hybrid index' by scoring individual plants for their degree of expression of selected characters thought best to differentiate the two presumed parents. It is apparently assumed that the characters used are controlled by several genes, and therefore show the 'blending' type of inheritance, the hybrids being more or less intermediate according to the contributions of the two parents. The potentialities of the method are considerable; in practice it is open to criticism in that subjective loading of the data is often necessary to obtain the desired result. The selection of the constellation of characters upon which to base the index is arbitrary, and the relative values attributed to them (expressed as a percentage of the total 'marks' allotted) has often to be decided subjectively. The technique can be refined, and thus made more capable of repetition by other workers, if the selection of the characters and the allowances to be made for their different variabilities are based upon statistics derived from preliminary studies of isolated populations of the parental forms in the manner already outlined. In the subsequent handling of hybrid populations, the maximum possible marks to be awarded to each character can then be made approximately inversely proportional to the mean of the coefficients of variation of the same character in the parental populations, and a more objective spacing of the hybrids thus ensured.

A previous speaker has drawn attention to the fact that if linear scales are used, the frequency distributions of measurements of cell size are generally found to be skew. This may also be so in frequency distributions of dimensions of macroscopic plant organs, of shape indices, and even of such characters as flower colour classes. Frequently the histograms become symmetrical when the character-expression scales are made logarithmic, and normal distribution can be assumed in further analysis.

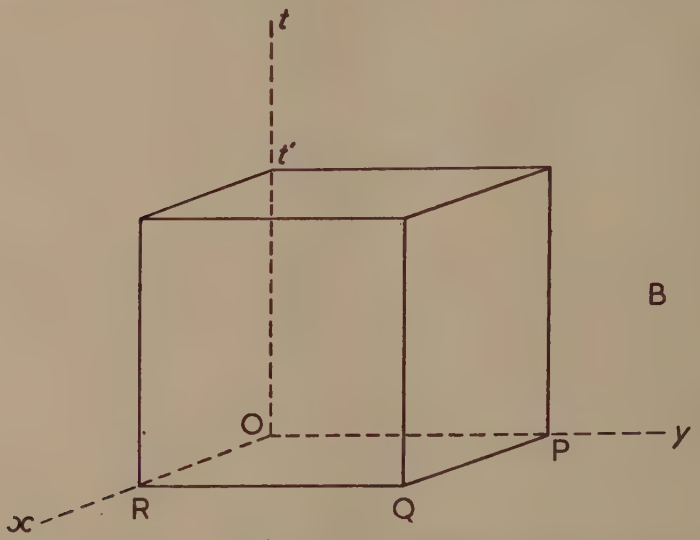
Finally, I should like to urge the desirability of keeping biometrical technique in its proper position in relation to orthodox taxonomy, as a tool to be used when needed. Not all systematists are mathematicians, and it is incumbent upon those who would attack critical groups with biometrical methods to ensure that at least their results are comprehensible to the non-mathematical systematist. As an aid to quick comprehension, the graphical treatments used as adjuncts to mathematical analysis by Anderson and others are admirable.

Dr. E. Trewavas: In considering Dr. Williams' curves of the frequencies of genera of different sizes, one is struck by the large numbers of monotypic genera. If there is an objective reality behind the generic groupings, it should be the reality of comparable degrees of relationship. It is relevant to ask whether the species that are given the rank of monotypic genera are always more distantly related to one another than are those that are grouped into large genera, or whether their differential characters are merely more striking to the museum worker. I think of a group of Nyassa species of fishes that are closely similar in most characters, yet each species has a characteristic dentition that has led to its being ranked as a monotypic genus. Other monotypic genera are the end-terms of undefinable groups of species of a large genus. Thus even the monotypic genera are heterogeneous, and it would seem doubtful if such an assemblage is amenable to statistical treatment.

Dr. Hopwood suggested that some of the difficulties encountered by palaeontologists are due to the fact that they commonly equate thickness with time, and substitute t for z in the normal Cartesian co-ordinates. The idea that a species is a cross-section of a lineage is held in common by stratigraphers and neontologists; such a species may be represented diagrammatically as a square OPQR lying in the plane determined by the axes x, y. The palaeonto-

logist then labels the third, vertical, axis, which should be thickness (z), as though it were time (t), and regards a prism erected on the square as representing the course of evolution during the lapse of time Ot' of the species symbolized by OPQR. This would appear to be an error based on a misunderstanding of the underlying factors.

The square OPQR represents a species in motion, that is to say, a species which is expending energy in the preservation of its identity, and the prism a species which has preserved its identity for the length of time Ot'. If, for example, the square be taken as a symbol of *Equus caballus*, and Ot' as the length of the Pleistocene, then the prism symbolizes the persistence of the horse



(Diagram from *Taxonomy Lectures* (Linnean Society) 1949–50, p. 29.)

throughout the Pleistocene; but if the square be taken to represent a primitive species of equine, the prism does not and cannot symbolize the evolutionary history of that species during a given period of time.

Although the point may not be of itself biometrical, it is not without significance in the interpretation of the raw material to which statistical methods are applied.

Dr. B. P. Uvarov said that biometrics are now coming into increasing use in insect taxonomy, particularly in the studies of infra-specific variation. An example of very fruitful application of biometrics to taxonomy is offered by locust phases, i.e. morphologically distinct forms of a species which are due to density of a breeding population. The existence of reliable morphological criteria for distinguishing the phases was obtained with the help of biometrics, and a biometrical technique has been elaborated, which is used in field studies, where it helps in assessing a tendency towards swarming as shown by changes in measurements and ratios of the individuals.

In applying biometric technique to taxonomy, one has to bear in mind that it is merely a tool, if a very useful one, but it should not be expected to provide automatic decisions. In fact, while a careful and critical use of biometric methods can help a taxonomist, it is also easy to become fascinated by formulae and graphs to the extent of forgetting the organism from which they have been derived.

PROCEEDINGS OF THE GENERAL MEETING ON 27 April 1950

Professor F. E. Fritsch, F.R.S., President, in the Chair.

The Proceedings of the General Meeting held on Thursday, 23 March 1950, having been circulated, were taken as read and confirmed.

The President, welcomed the presence at the meeting of Dr. Lindt, Cultural Attaché of the Swiss Legation.

The following were thanked for gifts made to the Library since the last Meeting:—Dr. T. E. T. Bond, Dr. L. Chalk, Dr. H. C. D. de Wit, Mr. Laurence Dopson, Prof. R. R. Gates, F.R.S., Dr. C. R. Metcalfe, Mr. Richard Morse, Mr. A. E. Porsild, Mr. Christopher Sandeman, Prof. James Small, Prof. J. L. B. Smith, Mr. W. T. Williams and the Trustees of the Transvaal Museum, Pretoria.

The President announced the publication in pamphlet form of the Lectures on the Development of Taxonomy delivered in the Rooms of the Linnean Society during the Session 1948–49.

Read for the first time certificates of recommendation for election to Fellowship in favour of A. A. Sandosham, L.M.S., Bangalore Gundappa Lakshoninaragana Swamy, D.Sc., Peter Karel Sartory, Charles William James Unwin, Richard Evans Schultes, Ph.D., Mrs. Ellen Hazelwood, Miss Mary Rosalie Jane Edwards, B.Sc., and Mr. Bertram Hanmer Bunbury Symons-Jeune ; and as an ordinary Associate, in favour of Miss Margaret Molson Parker.

Read for the first time certificates of recommendation for election to Foreign Membership in favour of the Rev. Father Pierre Teilhard de Chardin, S.J., of the Galérie de Paléontologie, Jardin des Plantes, Paris ; Prof. Dr. Jean Feldmann, of the Faculty of Science, Sorbonne, Paris ; Prof. Ernst Gäumann, of the Federal Institute of Technology, Zurich ; Mr Johannes Gossweiler, of Luanda, Angola ; Prof. Sven Otto Hörstadius, of the Royal University, Uppsala ; and Dr. René Jeannel, of the Laboratoire d'Entomologie, Muséum National d'Histoire Naturelle, Paris.

Candidates for membership were balloted for and elected :—

Fellowship.—Michael Marchmont Anderson, B.Sc., Leslie John Bartlett, D.F.C., Margaret Constance Helen Blackler, B.Sc., Ph.D., Helen Margaret Bance, B.Sc., Ph.D., Gordon Edgar Barnes, M.A., A.L.S., Arthur James Cain, M.A., D.Phil., William A. Clark, Ph.D., M. Dharmarajan, M.A., M.Sc., Ph.D., Felix Oladejo Dosekun, B.A., Hubert Frederick Dovaston, David Etherington, M.Sc., Miss Elizabeth Margaret Ewing Forsyth, B.Sc., Harold Gorvett, B.Sc., Ph.D., Edward Gurr, Michael Haworth-Booth, Kenneth John Hodges, B.Sc., Arthur John Ivens, Frederick George Brook Jones, M.A., Prakash Chandra Joshi, M.Sc., Ph.D., Derek Kellas, M.C., B.Sc. (For.), Mrs. Doris Mary Kermack, B.Sc., Francis Philip Knight, Miss Sheila Mackenzie Lodge, B.Sc., Ph.D., Alicia Lourteig, Kenneth Macleay, B.Sc., Ph.D., Frederick Gustav Meyer, B.S., M.S., Ph.D., Charles Clayton Mountfort, M.A., Tohamy A. A. Moussa, M.Sc., Miss Linda Mary Newton, B.Sc., Max Leopold Robert Pettersson, M.A., Ph.D., Nial Reynolds, B.Sc., Ph.D., William Herbert Ebenezer Rivett, Jack Roberts, B.Sc., Patrick Joseph Lindsay Roche, M.R.C.S. (Eng.), L.R.C.P.

(Lond.), Ernest Rouleau, Ph.D., Jack Marris Rowson, M.Sc., Ph.D., Ph.C., Gordon Ernest Williams, M.Sc., Ronald Frank James Withers, M.Sc., Bryan Sidney Young, B.Sc.

Ordinary Associateship.—Miss Joan Bain, B.Sc., Miss Ailsa McGown Clark, B.A., Frank Nigel Hepper, George W. Shaw, Denys William Tucker, B.Sc., Alan Wesley, B.Sc., A.R.C.S.

The President reported the deaths of Miss Emilia Frances Noel, Mr. Reginald John Chittenden and Mr. John Brooke Scrivenor, I.S.O., Fellows of the Society.

The following communications were read and discussed :—

Prof. Otto Jaag, F.M.L.S. The more recent developments in the biology of the Swiss lakes. (Discussed by the President, Dr. E. B. Worthington, Prof. G. R. de Beer, F.R.S., Dr. R. W. Butcher and Dr. F. Greenshields ; Prof. Jaag replied.)

Abstract,—

All Swiss lakes were originally of the oligotrophic type. During the past hundred years, however, a number of them have undergone a catastrophic development. Sudden enormous increases in the number of planktonic algae (*Oscillatoria rubescens*, *Microcystis aeruginosa*, etc.) have led to decreased penetration of light and to changes in the colour of the water.

Simultaneously, important chemical changes have taken place, such as loss of oxygen in the lower strata of the lake, and poisoning of the lake bottom through production of hydrogen sulphide, ammonia, and methane, products of the anaerobic decomposition of plankton organisms. At the same time a steady deterioration in the fish life became apparent. White-fish (*Coregonus wattmannii*) lakes were converted into lakes containing fish of inferior quality. Thus, biologically speaking, Swiss lakes such as those of Murten, Baldegg, Hallwyl, Zurich, Zug and Rotsee may be regarded as unbalanced lakes.

Swiss limnologists explain this condition as being the result of the increased rate of fertilization of the lakes by polluted waters from nearby villages, cities, and factories. The organic and inorganic wastes enrich the lakes and result in an increase in the plankton. Growth and decomposition of the disproportionately large quantities of plankton lead to new environmental conditions which are unfavourable for the more valuable species of fish.

An energetic movement has developed for the preservation and protection of the Swiss lakes and streams through the establishment of better methods of waste disposal.

Discussion,—

Dr. F. Greenshields: Eutrophication of fresh waters is presenting some of us in Britain with problems akin to those described by Professor Jaag for some of the Swiss lakes, especially in our lowland districts.

Certain reservoirs in the London area have also borne dense crops of *Oscillatoria rubescens* and experience with them over a number of years has created in my mind a strong impression that simple eutrophication is not enough to account for its proliferation and that there also exists a necessary connection with anaerobic breakdown of settled organic matter. Some of the ecological situations encountered further suggest a correlation with the energetics of a sulphur cycle.

Whatever is the true nature of the relations there can be little doubt of the existence of circumstances so peculiarly favourable to *Oscillatoria rubescens* as to characterize some lakes as " *O. rubescens* lakes ".

Calculations I have made using data published by the Swiss limnologists E. A. Thomas and E. Märki about Lake Zurich and some obtained from a reservoir in south-east England suggest that if our Swiss friends wish to inhibit algal growth, especially *O. rubescens*, in Lake Zurich by starving the algae of nitrogen, as has been proposed elsewhere, they may have to aim at preventing the access of not less than 98% of the amount now entering the lake. Something of the magnitude of such a task may be gleaned by recollecting the main facts known of the nitrogen cycle in nature, the high solubility of the nitrates, and the resistance to adsorption shown by the nitrate ion, and the suspicion that *O. rubescens* and some other planktonic Myxophyceae can and do fix elemental nitrogen.

With regard to mud profiles such as those taken by F. Nipkow and to which Professor Jaag has referred I would only like to say that whereas the dark and light banding may be correctly interpreted in this instance as representing paired annual events in the lake's past great care should be taken whenever like banding is observed in muds lest stratification resulting from a single event in time is mistaken for an historic sequence. Transient rhythmic Ord-Liesegang precipitation of crystals of aragonite and calcite is occasionally observed in clayey muds and I have frequently induced the same effect in a clear and colourless lake water by slightly increasing the concentration of hydroxyl ions.

Dr. E. B. Worthington. Zoological and Botanical Research in Eastern Tropical Africa. (Discussed by the President, Prof. G. D. Hale Carpenter, M.B.E., and Dr. W. B. Turrill.)

ZOOLOGICAL AND BOTANICAL RESEARCH IN TROPICAL AFRICA

By E. B. Worthington
(Scientific Secretary, East Africa High Commission).

(Extended abstract.)

The object of this paper is to explain some of the facilities for biological research which now exist, especially in British East Africa. In doing so emphasis is laid on the need for a taxonomic and systematic background as an essential basis for the economic kind of biological science on which most colonial workers are bound to concentrate at the present time.

In the old-established countries—Europe and North America—more than a century of study was devoted to plants and animals before 'modern biology', including physiology, genetics and ecology, came into existence as independent subjects. Meanwhile an extensive background of systematic and structural knowledge was accumulated. But tropical Africa, with its more diverse environment and greater variety of form in plants and animals than any similar area of the old countries, has been subject to systematic studies for a much shorter period and by far fewer workers. Most biologists in tropical Africa have used 'modern' disciplines and techniques, so that to-day there is a considerable superstructure of biology built on no secure systematic foundation.

In conditions of the colonies, where the number of biologists is relatively few and the individuals are apt to be widely scattered, there are obvious advantages in pooling resources and in arranging a division of labour over a wide area. This is being achieved for the region of British East Africa through the agency of the East Africa High Commission. The system works as follows.

The region consists of four separate countries—Kenya, Tanganyika, Uganda and Zanzibar—and each of their Governments has its own technical departments which include, on the biological side, agricultural, veterinary, game and medical departments, and in some cases separate departments for the control of tsetse-flies. Many of these departments have their own groups of specialist biologists

who are necessarily devoted primarly to problems of direct economic importance. In addition to the territorial governments, the East Africa High Commission has established a number of scientific and research departments which operate throughout the whole region, and, being exempt from day to day advisory work, are able to take a longer view of research problems. Some of these have very wide functions; there is for example, an Agriculture and Forestry Research Organization, a veterinary Research Organization and a Fisheries Research Organization. Others are more restricted in their field, such as the Tsetse and Trypanosomiasis Research and Reclamation Organization and the Desert Locust Survey, the latter conducting biological work in a number of countries to the north of East Africa, whence come the invasions of locusts. Some of these inter-territorial scientific organizations and departments—there are ten of them in all—are new and just getting into their stride. Others are based on pre-existing foundations. In agriculture, for example, there is the old Agricultural Institute at Amani in Tanganyika, which is based on buildings, collections and an important library established there by the Germans before the 1914–18 war ; and for tsetse research there has been for many years the research centre at Shinyanga, south of Lake Victoria.

One important institute which comes outside the direct Government sphere is the Coryndon Museum in Nairobi. This is self-administered by a Board of Trustees, and, like other museums, is usually short of funds, but it is developing steadily as a principle centre in East Africa for systematic biology. It has a small permanent staff devoted to various branches of biology and also a considerable section on archaeology. There are other museums also : the Uganda Museum which is concentrating mainly on ethnology, the Tanganyika Museum at Dar-es-Salaam, and the Zanzibar Museum. Then there is the budding University of East Africa, Makerere College in Uganda, with a number of departments undertaking research as well as training, including a biological department, and there are other agencies, notably the Empire Cotton Growing Corporation and the Overseas Food Corporation which are conducting important research in biological subjects.

Many of the institutes and organizations mentioned, including all of those coming under the aegis of the East Africa High Commission, are financed, at least in part, from funds voted by the British Parliament under the Colonial Development and Welfare Acts of 1945 and 1949. It is appropriate here to mention a few specific projects in biology, more especially concerned with systematics, and financed from the same source.

There is no ' Flora ' of East Africa. Botanists working there have felt the lack very acutely and, backed by botanists at Kew and elsewhere, have made recommendations about it frequently during the past twenty years. Clearly for the preparation of an East African Flora, Kew Gardens is the practical as well as the spiritual base, and arrangements have been made for the appointment to Kew of six additional botanists to devote themsleves primarily to this purpose. The intention is that one of the six will work in East Africa each year to study his speciality in the field. Side by side with this scheme, another has provided for a regional herbarium in East Africa itself. The new building is now complete, in the grounds of the Coryndon Museum, and in it will shortly be incorporated the two main herbaria already existing there, the Amani herbarium and the Coryndon herbarium, in order to provide one comprehensive and efficient base for plant taxonomy in the region.

Another example of a recent project is one for research on that big insect group, the Termites, which are of far-reaching economic importance in tropical agriculture as well as being agents of destruction to buildings and all structures made of wood. In this case the project is concerned with the whole Colonial Empire, but the work has started with East Africa.

Fisheries and hydrobiology is another good example, comprising systematic

as well as ecological and economic studies. There is now established on the north shore of Lake Victoria, at Jinja where the Nile has its origin from the lake, a new laboratory as the headquarters of the East African Fisheries Research Organization. It has facilities in the way of launches and a growing supply of equipment and of scientists. In addition there is a high level research centre for the biology of streams on the slopes of Mount Kenya, and plans are developing for another station on Lake Tanganyika. These three stations will provide unrivalled facilities for all aspects of tropical freshwater biology, and there are also plans now reaching fruition for a marine fisheries research centre at Zanzibar.

Turning westward, to the continuation of the equatorial belt in the Belgian Congo, we see a considerable expansion of facilities for biological research which parallel in some respects those of British East Africa. Our relations with the Belgian scientists are extremely good and contacts are becoming more frequent. They have had for a good many years, a big agricultural research organization —I.N.E.A.C.—with branches in the major ecological and economic zones of the Congo, and also their unique organization for the National Parks, in which many biological, and especially systematic studies have been arranged. Now, to complete the picture, the Belgians are actively engaged in establishing I.R.S.A.C. (Institut de Recherche Scientifique en Afrique Centrale) with a number of centres which will be concerned with fields other than those directly concerned with agriculture.

Thus the picture of research facilities in Africa today is very different from that of ten or even five years ago. In addition to the headquarters and main laboratories of the various organizations, there is a good number of field stations distributed across the equatorial belt. Although they are designed for specific purposes and many have a bias towards research of practical value in colonial development, they are continually throwing up problems of a truly fundamental kind and not infrequently concentrating attention on such problems. Some of the new centres are not yet complete, and many are not yet fully staffed, but they have reached the stage when their directors welcome *bona fide* scientific visitors coming to conduct research of a kind which can only be done in the tropics. Indeed there is a growing number of such visitors from universities and institutes in Europe. The tropics, so long neglected as a field for zoological and botanical research, may soon come into their own.

PROCEEDINGS OF THE GENERAL MEETING ON 11 May 1950

Professor F. E. Fritsch, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 27 April 1950, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Dr. Agnes Arber, F.R.S., Prof. W. H. Pearsall, F.R.S., Prof. Dr. C. Wesenberg-Lund, F.M.L.S., the Chilean Iodine Educational Bureau, London, and the Marine Biological Station, Millport, Isle of Cumbrae.

The following Fellows signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Mr. Frederick Claude Deighton, O.B.E., Prof. Alan Robertson Gemmell, Mr. David Etherington, Mrs. Doris Mary Kermack, Mr. Charles Clayton Mountfort, Mr. Kenneth John Hodges, Mr. Leslie John Bartlett, D.F.C., Mr. Ronald Frank James Withers.

The President reported the death of Professor Oakes Ames, Fellow of the Society.

Read for the second time certificates of recommendation for election to Fellowship in favour of A. A. Sandosham, L.M.S., Bangalore Gundappa Lakshoninaragana Swamy, D.Sc., Peter Karel Sartory, Charles William James Unwin, Richard Evans Schultes, Ph.D., Mrs. Ellen Hazlewood, Miss Mary Rosalie Jane Edwards, B.Sc., and Mr. Bertram Hanmer Bunbury Symons-Jeune.

Read for the second time certificates of recommendation for election to Foreign Membership in favour of the Rev. Father Pierre Teilhard de Chardin, S.J., Prof. Dr. Jean Feldmann, Prof. Ernst Gäumann, Mr. Johannes Gossweiler, Prof. Sven Otto Hörstadius, and Dr. René Jeannel.

The following communications were read and discussed :—

Dr. Hugh Scott, F.R.S. Journey to the Gughé Highlands (Southern Ethiopia). (Discussed by Prof. G. D. Hale Carpenter, M.B.E., Mr. C. N. Hawkins, Dr. W. B. Gourlay and Dr. S. E. Chandler, O.B.E. ; Dr. Hugh Scott replied.)

Abstract,—

In central and southern Abyssinia isolated mountains and massifs rise from plateaux at 6,000 to 8,000 feet to heights of from 10,000 to over 13,000 feet. Like the still higher mountains of east and central Africa, most are volcanic cones, or massifs of igneous rocks, related to the Rift Valley fault-system.

Largely as the result of an earlier journey (1926–7), certain faunistic peculiarities are evident. The higher zones of the Abyssinian and east African mountains form cool, moist 'islands' separated by relatively dry tropical plateaux. As centres of prolific speciation their rôle is analogous to that of some oceanic islands. Certain genera are represented by series of species confined each to a particular massif, and in some groups distinct lineages are traceable ; e.g., two main lines of descent appear to have met in the sub-family Trechinae (Carabidae, Ground-beetles), their branches interlock but remain distinct. One is related to the north-temperate fauna ; the other has affinities with South Africa and even with the sub-antarctic Crozet Archipelago.

Biogeographically, Abyssinia is still largely unknown. Some parts have been sketched in from data obtained on visits (1926) to the extinct volcano Zuquala (9,900 feet) and the Chillalo massif (13,100 feet), respectively S. and S.E. of Addis Ababa. The principal goals in 1948 were the isolated Mt. Damota (10,400 feet), N.W. of Lake Margherita (Abaya), and Mts. Tola and Gughé in the Gughé Highlands complex (believed to reach over 13,700 feet) immediately W. of the lake. Their topography has not been fully described, and many of the slides illustrated the countryside and people.

The crops found highest on the steep, closely cultivated slopes are Ensete trees (resembling banana trees at a distance), barley, and potatoes. Lofty bamboos, principal remnant of the almost vanished forests, are confined to neatly fenced groves in the least accessible places. Only the mountain tops are uninhabitated : they are peat-lands covered with alchemillas, tree-heaths, *Kniphofia* spp., etc. The southern slopes have been less deforested, and the return route northward, to the east of Lakes Chamo and Margherita, traversed extensive forests, mainly of giant *Podocarpus*.

The people are diverse and closely segregated. The Cushite groups in the formerly independent states comprising the provinces of Wolamo and Gamo, west of the lakes, and the Nilotic negroes of Konso in the S.E., speak tongues

unknown to most Ethiopians. Their agriculture and other occupations were illustrated; also wayside monuments of Galla warriors, and monoliths ascribed to an ancient phallic cult.

[A full paper will be printed in a forthcoming Part of the Proceedings.]

Dr. F. C. Fraser. Diverticula of the eustachian tube of Cetaceans. (Discussed by Prof. A. J. E. Cave, Mr. P. E. Purvis, Dr. H. W. Parker, Mr. N. B. Marshall and Mrs. D. M. Kermack; Dr. Fraser replied.)

Abstract,—

It has long been known that in Cetacea, and especially in toothed whales, the eustachian tube forms a complicated system of diverticula and ramifying branches. Until methods of injection with plastics were available, the system could not be disentangled from the adjoining blood-vessels and oil-ducts. Application of the new technique demonstrates the extent and finer detail of the eustachian system.

[A full paper will be printed in a forthcoming Part of the Proceedings.]

The following paper was read in title :—

' Some further Davall records '. By Dr. G. R. de Beer, F.R.S., F.L.S. (Printed in full, below.)

SOME FURTHER DAVALL RECORDS

By Dr. G. R. de Beer, F.R.S., F.L.S.

In a former publication (Proc. Linn. Soc. Lond. *159*, 1947, p. 44) I drew attention to the fact that the Proceedings of the Private Society of Friends of Natural History in Berne contained numerous references to Davall. Through the kindness of Dr. Strahm, Librarian and Archivist of Berne, I have had the opportunity of studying these from photostats, and some of them appear to be of sufficient interest to justify publication here.

The Proceedings of the meeting held on 29 June 1787, contain a list of indigenous Swiss plants additional to those published by Haller in his great work. The list is as follows :—

List of some plants of Switzerland which were not included in the Historia Plantarum of Baron von Haller.

1. Alisma Ranunculoides. Mr. Dick.
2. Dianthus arenarius. Mr. Morell.
3. diminutus ? Mr. Haller.
4. Poa rigida. Mr. Lorimier d'Aubonne.
5. Scirpus Holoschoenus.
6. Euphorbia falcata. Mr. Reynier ?
7. Vaccinium mucronatum. Mr. Morell.
8. Vicia peregrina ? ? Herbier de Thomas.
9. Draba ? Thomas.
10. Spartium purgans ? Thomas.
11. Draba pyrenaica. Dr. Girtanner.
12. Geranium pyrenaicum ?
13. Genista decumbens. Mr. Morell envoyé par Thomas.
14. Potentilla alba. Mr. le Min. DuCloz [*sic, recte* Du Cros] dans les bois de Praugin.
15. Ulex Europaeus. Mr. Lorimier.
16. Hypochoeris maculata. Mr. Gagnebin.
17. Cerinthe minor. Mr. Lorimier.

Hibiscus Trionum ? ? trouvé dans le Vallais par Favrod de Château d'Oex.

[Added in pencil :] Tordylium maximum. Tragopogon majus.

The Proceedings of the meeting held on 26 October, 1787 contain a list of the plants which, in the company of Davall, the younger Haller found in the course of an expedition to the Bernese Alps in the neighbourhood of Kandersteg.

Enumeratio Plantarum rariorum, quas Comite Davall, Botanophylo Anglo, invenit Diebus 31 Jul. et 1 Aug. 1787. Alb. Haller, fil.

In Loco, die Claus, qua Vallis Gastern aditur.

Plantae rariores.

Saxifraga caesia.
caespitosa.
Leontodon aureum.
Thlaspi Saxatile.
Pedicularis foliosa.
verticillata.
Lepidium alpinum.
Silene quadrifida.
acaulis.
Arabis alpina.
Arenaria saxatilis.
Cistus marifolius, s. oelandicus.

Plantae vulgariores.

Biscutella didyma.
Thymus alpinus.
Saxifraga Cotyledon. Var. α et floribus aurantiis.

In ipsa valle, inter Clus et Casas pastorias.

Arenaria dichotoma.
Hedysarum obscurum.
Hieracium 42—humile Jacq.
alpestre Jacq.
Astragalus campestris.
montanus.
Silene rupestris.
Empetrum nigrum.
Bupleurum angulosum.
ranunculoides.
Arnica Scorpioides.
Sedum atratum.
Scheuchzeri.
Geranium subcaeruleum.
Achillea atrata.
Euphras. offic. flore luteo.
Pyrola uniflora.
Aster alpinus.
Erigeron alpinum.
uniflorum.
Sempervivum arachnoideum.
tectorum.
Mespilus Cotoneaster.
Senecio Doronicum.

Geranium sylvaticum prata potissimum effecit.

Anemone alpina.
Arctium Personata.

Circa moles Glaciales, in lapidibus deciduis & ad radices Montis Schilt.

Ranunculus alpestris.
glacialis.
Gentiana nivalis.
Amarella.
Trifolium alpinum.
Astragalus alpinus.
Phyteuma hemisphaerica.
rhaetica. Variet. notabilis.
Rumex digynus.
1598.
Potentilla grandiflora, abunde.
Sibbaldia procumbens.
Achillea macrophylla.
Saxifraga androsacea.
aspera.
bryoides.
cuneifolia.
oppositifolia.
Potentilla aurea.
Imperatoria.
Phellandrium Mutellina.
Bartsia.
Trifol. Spadiceum.
Athamanta Libanotis.
cretensis.
Phleum alpinum.
Azalea procumbens.

Pedicularis rostrata.
tuberosa.
Anthericum serotinum.
Viola calcarata.
Juncus trifidus.
luteus.
Aquilegia alpina.
Cardamine resedifolia. bellidifoliam non inveniri potuit.
Laserpitium simplex.
Graphalium alpinum.
Arnica montana.
Anemone alpina flore luteo.
Salix reticulata.
retusa.
arbuscula ?

In the Proceedings of the meeting held on 30 May 1788, is a further list of plants which Davall had sent to Haller (partly translated here) :—

Spartium Scoparium. inter Dizier et Romainmôtier.
Dianthus Virgineus β. L. sur la roche blanche près d'Orbe.
Spartium radiatum. sur le Mont Verné. Thomas had taken this plant to be Sp. purgans and it appears under this name in the list given above until Mr. Davall corrected its determination.
Silenum Chabraei. apud Romainmôtier. M. de la Chenal had already found it near Basle and described it. Acta Helvetica, Vol. VII. p. 334.
Hieracium humile Jacq. Fl. Austr. t. 189. Gasternthal.
Ulex Europaeus. near Aubonne.

The copy of the elder Haller's *Nomenclator* (referred to in Proc. Linn. Soc. Lond. *160*, 1948, p. 179) contains a number of entries made by Davall in his own handwriting giving the habitats of a number of plants which he had collected in the course of his numerous journeys.

In the following list the numbers are those of Haller (*Nomenclator*, 1769) followed by Haller's *Generic Names*. To these are added in square brackets Davall's specific epithets as written in the margin. Where Davall has written a different generic name it is included. Finally, in spare brackets are added Davall's habitats.

Davall's record of habitats of Swiss plants, made in his copy of Haller's Nomenclator, 1769.

2. Hypochoeris [helvetica] [refers to H. maculata—haec maculatâ abundè inveni circa St. Pièrre]
27. Picris [Hieracium Taraxaci] [Gemmi]
38. Hieracium [montanum] [Dôle]
54. Hieracium [florentinum Allioni] [circa Leucam Valesiae ?]
66. Senecio [paludosus] [pond of Arnex]
88. Doronicum [Pardalianches] [M. Salève]
89. Arnica [Scorpioides] [Graphengel]
112. Achillea [moschata Jacq.] [ad fontes Rhodani. D.]
113. Achillea [nana] [Furca. St. Bernard & circa glacialia Valsorey]
126. Apsinthium [rupestris ? non L.] [Grindelienses Gäbuse vocant]
127. Artemisia [spicata] [Roche Poli and Valsorey]
144. Chrysocoma [Linosyris] [Valesiae]
152. Filago [Leontopodium !] [Gemmi, Dolaz]
200. Dipsacus [Scabiosa alpina L.] [prope St. Cergue inveni 1785. D.]
226. Mentha [rotundifolia] [inter Lausanne & Vevay]
316. Pedicularis [recutita] [Furca]

333. Antirrhinum [Orontium]	[on walls at Vevey, Berne and Geneva]
339. Antirrhinum [Cymbalaria L.]	[at Sion, Altorf; etiam Lucernae in muris, immensa copia]
371. Trifolium [scabrum]	[Nion]
379. Buceras [monspeliaca]	[sub arcem Octodurum. E.D.]
451. Arabis [alpina]	[ubique in muris vetustis Urbae]
462. Eruca [Sisymbrium arenosum]	[legi ad viam regiam prope Champlitte ? or Vesaigne?]
481. Sisymbrium [dentatum Allioni.]	[St. Bernard]
488. Alyssum [Sisymbrium pyrenaicum]	[in summa Valesiae ad viam]
490. Alyssum [Myagrum saxatile]	[in alp: scabra inv:]
573. Pervinca [major]	[Orbe]
622. Aretia [Androsace lactea]	[supra Bulet à la Roche bla[n]che]
624. Androsace [maxima]	[circa Urbam. D.]
638. Gentiana [punctata]	[Furca. D.]
639. Gentiana [purpurea]	[Furca. immensa copia. D.]
683. Rapunculus [sine epithet. spec.]	[near Leuck]
771. Bupleurum [stellatum]	[circa Pontem Diaboli]
804. Selinum [Athamanta Cervaria]	[circa Urbam abundè]
811. Tordylium [maximum]	[near Orbe. D.]
817. Ribes [alpinum]	[Orbe]
881. Alsine [Stellaria hypericifolia Allioni]	[Furca. circa fontes Rhodani]
890. Myosotis [Stellaria cerastoides]	[St. Bernard copiosissimè]
1018. Arbutus [Uva ursi]	[etiam in planitei circa Arnex]
1114. Fragaria [Potentilla grandiflora]	[Gasternthal. D.]
1151. Anemone [fragifera]	[Gemmi]
1230.*Hemerocallis [fulva]	[in Valesia inf: inter Martigny & St. Pièrre ? going to Sion]
1252. Narcissus [Pseudo-Narcissus]	[I have gather'd it in abundance beyond Pontarlier but not yet in Switzerland.—since on the Dôle]
1434. Festuca [decumbens]	[in lapidosis Suchet. Hall:]
1517. Arundo [Melica ciliata !]	[at Orbe & alibi]
1546. Cynosurus [echinatus]	[inter Lax et obergestelen Vales. sup. D.]
1568. Alchemilla [pentaphyllea]	[Furca. abundè]
1585. Chenopodium [Botrys]	[Tourtemagne, Pompaple]
1687. Struthiopteris [Osmunda Spicant]	[Foot of the Furca on the Vallais]
Addition, without a Hallerian number :—	
Trifolium caespitosum Reyn.	[in Gemmi reperi]

PROCEEDINGS OF THE ANNIVERSARY MEETING
24 May 1950

Professor F. E. Fritsch, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 11 May 1950, having been circulated, were taken as read and confirmed.

The following Fellows signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Dr. Helen Margaret Bance, Mr. Frederick Flippance, Miss Elizabeth Margaret Ewing Forsyth, Dr. Maud B. E. Godward, Mr. Edward Gurr, Dr. Alicia Lourteig, Dr. Frederick Gustav Meyer, Miss Linda Mary Newton, Dr. Max Leopold Robert Pettersson, Dr. Nial Reynolds, Dr. Jack Marris Rowson and Mr. Gordon Ernest Williams.

Candidates for membership were balloted for and elected :—

Fellowship.—Miss Mary Rosalie Jane Edwards, B.Sc., Mrs. Ellen Hazelwood, A. A. Sandosham, L.M.S., Peter Karel Sartory, Richard Evans Schultes, Ph.D., Bangalore Gundappa Lakshminarayana Swamy, D.Sc., Bertram Hanmer Bunbury Symons-Jeune and Charles William James Unwin.

Foreign Members.—Rev. Father Pierre Teilhard de Chardin, S.J., Prof. Dr. Jean Feldmann, Prof. Ernest Gäumann, Johannes Gossweiler, and Prof. Sven Otto Hörstadius and Dr. René Jeannel.

Ordinary Associate.—Miss Margaret Molson Parker.

The Bye-Laws regulating the election of Council and Officers having been read by the Assistant Secretary, the PRESIDENT declared the Ballot for new Members of Council to be open, and voting began. The PRESIDENT thereafter appointed Dr. W. B. TURRILL, Dr. J. K. SPEARING, and Mr. J. R. SEALY, as Scrutineers of the Ballot.

The Ballot was closed at the due time, and the result declared to the Meeting. NEW MEMBERS OF COUNCIL.—Mr. Gerald A. Best, Dr. S. E. Chandler, O.B.E., Dr. I. Gordon, Mr. C. E. Hubbard and Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S.

(The retiring Councillors were Dr. E. B. Ford, F.R.S., Dr. S. M. Manton, F.R.S., Dr. H. W. Parker, Prof. W. H. Pearsall, F.R.S., and Dr. W. B. Turrill.)

The PRESIDENT declared the Ballot for Officers to be open and voting began. The Ballot was closed at the due time, and the result declared to the Meeting. OFFICERS.—*President*: Professor F. E. FRITSCH, F.R.S.; *Treasurer*: Colonel F. C. STERN, O.B.E., M.C.; *Botanical Secretary*: Dr. B. BARNES; *Zoological Secretary*: Dr. A. TINDELL HOPWOOD.

The PRESIDENT then called upon Mr. HENRY N. RIDLEY, C.M.G., F.R.S., F.L.S., who had been selected as the recipient of the Linnean Gold Medal, and referred to the recipient's great services to botany. In reply, Mr. Ridley expressed his profound appreciation of the honour that had been conferred upon him.

In handing the Linnean Medal to the recipient, the PRESIDENT spoke as follows :—

Mr. Ridley: In awarding to you the Linnean Gold Medal this Society not only honours one who has occupied a very distinguished position among the taxonomic and economic botanists of three generations, but one who has been a Fellow of this Society for well nigh seventy years. It is now more than sixty years since you were appointed Director of Gardens and Forests in the Straits Settlements, with headquarters at Singapore. At the time when you took up this post the Malayan flora was largely unknown, but thanks to the prodigious energy with which you proceeded to explore it, the plants of this region may now be ranked as comprising one of the best known of tropical floras. The specimens you collected from all parts of the Peninsula and the adjacent islands form important components of the herbaria at Kew, the British Museum, Calcutta and Singapore, while many living plants were sent to Kew or grown in the Singapore Gardens which soon ranked among the richest of their kind. After your retirement in 1912 you continued to add to your private herbarium by expeditions to the Tropics and most of this material, comprising about 50,000 specimens you have worked out yourself in the Herbarium of the Royal Botanic Gardens, Kew, where most of your types are lodged.

Apart from this stupendous contribution to the knowledge of the tropical flora, botanical science is indebted to you for many important works and scientific papers in which you have laid down for the benefit of posterity the results of your prolonged and varied researches. Chief among these rank the three volumes on Monocotyledons published in 1907, the book on Spices which

appeared in 1912, the *Flora of the Malay Peninsula* completed in 5 volumes some 25 years ago, and the book on the *Dispersal of Plants throughout the World*, so valuable to botanists in general, that was produced in 1930.

In the economic field also your services have been of the utmost value. It was largely as a result of your initiative that *Hevea* was established in the eastern Tropics and that the enormous development of the plantation rubber industry ensued in that part of the world. The method of tapping the trees which you devised played no small part in the successful foundation of this industry.

The manifold services that you have rendered to mankind and to botanical science have already met with wide-spread recognition. In 1906 the annual volume of the *Botanical Magazine*, in which so many of the plants collected by you have been figured and described, was dedicated to you. In 1907 you were elected to the Fellowship of the Royal Society, in 1911 the distinction of Companion of the Order of St. Michael and St. George was conferred upon you, while in 1928 the United States Department of Agriculture awarded you the Frank N. Meyer medal for the role you played in the establishment of the *Hevea* industry in the oriental Tropics.

This Society now honours itself by including your name among those of the many distinguished botanists who have been recipients of the Linnean Medal.

The Librarian and Assistant Secretary presented his Report.

LIBRARIAN AND ASSISTANT SECRETARY'S REPORT

List of the Society.—Since the last Anniversary Meeting the Society has lost 30 members. The detailed statement is as follows :—

18 *Fellows by death.*—Oakes Ames, Edmund Gilbert Baker, Stephen John Batchelder, Reginald John Chittenden, George Henry Evans, C.I.E., C.B.E., Robert Gurney, Miss Ida Margaret Hayward, Robert Wilfred Inder, Miss Gulielma Lister, Sir Murdoch McLeod, Bt., Frederick William Mills, Sir Frederick William Moore, Kt., Miss Emilia Frances Noel, David Joseph Scourfield, I.S.O., John Brooke Scrivenor, I.S.O., Harold Walkden, Alfred James Wilmott, Albert Wilson.

6 *Foreign Members by death.*—Boris Aleksyevich Fedtschenko, René Maire, Paul Marchal, Alfred Rehder, Filippo Silvestri, Richard Woltereck.

6 *Fellows by Withdrawal.*—Florence Elizabeth Barnett, Harry Arnold Baylis, Peter John Bell, Sir Geoffrey Evans, C.I.E., Kenneth James Franklin, John Adams Pringle.

During the Session 47 Fellows, 6 Foreign Members and 9 ordinary Associates have been elected. The number of Fellows on the List is 778 with a further 22 Fellows elected but not yet qualified.

Library.—Between the 1 May 1949 and 30 April 1950, 24 books have been purchased ; 48 books, 135 parts of periodical publications and 54 reprints have been presented. During the same period the number of volumes bound was 529 and 438 volumes have been repaired.

The number of volumes borrowed by Fellows and Associates was 1014 and by the National Central Library 522. 567 signatures were recorded in the Library Visitors' Book.

Linnaean and Smithian Collections.—During the past year the Society's Collections have been consulted frequently. The compilation of the Catalogue of the Smithian Herbarium has been continued.

THE PRESIDENT'S REVIEW

The 162nd session of the Society which terminates to-day, has not been marked by any momentous happenings, although the Society has every reason to congratulate itself on the contribution it has made to scientific discussion and progress. For the first time for many years a former practice was renewed in the form of a Presidential reception, and I have only heard it spoken of as an unqualified success. A most interesting series of exhibits was shown on that evening, and Dr. George Taylor contributed greatly to the enjoyment of those present by exhibiting a colour film of Tibetan flowering plants. Seven of the General Meetings of the Society were discussion meetings, and all will agree that they were full of interest and that they excelled in the diversity of the topics dealt with. It is scarcely feasible to make a selection among them, but I think we all felt that the discussion on Morphogenesis, in which Professors Ashby, de Beer and Wardlaw participated, reached a level which has not often been surpassed. I may also recall the discussion on Morphology and Fine Structure and the joint discussion with the Systematics Association on Biometrics and Systematics, both of which seemed to me to be very fruitful and perhaps to call for further discussions on special aspects of these topics in the near future. On 27 April the Society enjoyed the rare opportunity of being addressed by one of its Foreign Members, when Professor Jaag spoke on biological conditions in the Swiss Lakes.

Since the last annual review there have been published two parts of the Zoology and one part of the Botany Journal; a second part of the latter is in the press. The two parts of Vol. 161 of the Proceedings have appeared and the first part of the new volume is now being printed. A pamphlet containing the lectures on the Development of Taxonomy that were given during the session 1948–49, was published at the end of April of this year, and the Council has decided that the Taxonomy Lectures delivered during the present session shall likewise be published as a separate pamphlet.

The Library continues to make good progress and the Restoration Fund has been augmented by the donation of the balance (£57) of the fund in the hands of the Trustees of the Imperial Botanical Conference held in 1935. It has been decided that the interest on the Legacy (of £1000) bequeathed by our late Fellow R. J. Flintoff, shall be used for the purchase of Library Books, such books to be provided with a special book-plate. The Library has been enriched by the gift of many books, some the work of Fellows of the Society. Among them I would particularly mention Dr. Agnes Arber's *The Natural Philosophy of Plant Form*, a work of outstanding interest and the result of many years of studious thought.

We have to deplore the death of eighteen of our Fellows, and six of our Foreign Members. Miss Lister and D. J. Scourfield had served on the Council and as Vice-Presidents of the Society, and the latter was in 1940 the recipient of the Crisp Award and Medal. A. J. Wilmott and E. G. Baker had likewise served on the Council, and the former was always an active participant at the Society's meetings and gave a valuable lecture in the Taxonomy course only the day before his tragic death.

At the meeting on 9 March a congratulatory message on his 70th birthday was sent to Dr. Reinhard Dohrn, Director of the Naples Marine Biological Station and Foreign Member of the Society. We have just received the following reply :—

> " To the PRESIDENT, COUNCIL, Fellows and Associates of THE LINNEAN SOCIETY OF LONDON.
>
> Dr. Reinhard Dohrn thanks the members of the Linnean Society for their kind greetings and good wishes on the occasion of his

70th Birthday. Dr. Dohrn is proud to remember his thirteen years association with the Society and the good relations that have always subsisted between it and the " Stazione Zoologica ". He hopes that the Institute will have the privilege of serving all members of the Society who may wish at any time to visit Naples.

(*Signed*) REINHARD DOHRN.

Naples, 8 May 1950.

Prof. James Small represented the Society at the Centenary Celebrations of Queen's University, Belfast, and I myself attended the recent Jubilee Celebrations of Birmingham University as your delegate. The Council have also appointed me as the Society's Delegate to the Seventh International Botanical Congress to be held in July in Stockholm. It has been agreed that the Society shall join the British Co-ordinating Committee for Nature Conservation.

In 1947 my predecessor announced that 100 new Fellows were still required to bring the Society back to the position which it occupied before the war. Thanks to his energetic action this has now been achieved and even markedly surpassed, and it became clear last Autumn that the 800 limit for the number of Fellows required revision. At the General Meeting on 21 November, Section 1, Chapter 1 of the Bye-Laws was amended to read : " The number of Fellows shall be limited to 1000, exclusive of Honorary Members Foreign Members and Associates . . . " At present our Fellows number slightly over 800, but it is very desirable that we should aim at reaching the 1000 limit, since this would enable us to produce our publications without having to seek financial help from government sources. The Treasurer will no doubt have more to say about this.

There is at present nothing to add to what my predecessor said at the last Anniversary Meeting respecting the creation of a special centre for Scientific Societies, except that the particular proposal to which he made reference has to the best of my knowledge been, temporarily at least, abandoned.

In conclusion I should like cordially to thank the Vice-Presidents, the Treasurer, the Secretaries, the Assistant Secretary and the Staff of the Society for the manifold help they have afforded me in conducting its affairs.

The Financial Report was given by the Treasurer and the Accounts of the Society, duly audited, for the year 1949–50 were laid before the meeting.

TREASURER'S REPORT

Printed copies of the Accounts for the financial year which ended on 30 April 1950 are before the Fellows. For comparison, the figures for last year are printed in italics on the left-hand side. A statement has been prepared by the Auditors who certify as to detail; the Audit Committee has inspected the books, verified the investments and bank balances and passed the Accounts; the action of the Committee has been confirmed by the Council.

I will briefly go through the accounts and deal with the main items :—

On the Income side the Admission Fees are lower due to fewer Fellows being elected than in the previous year, the Annual Contributions are up, due to the increased Fellowship. The Sales of publications are a little down on last year, but the Society has received £717, a considerable sum. The Society again received from the Royal Society the sum of £750 from the Parliamentary grant-in-aid for Publications. We are deeply grateful for this help to our funds for expenditure on publications. The Council has decided to place £700 to the Reserve for Publications for the coming year leaving a balance in the General Account of £709. The cost of publications has been less this year and unless

any unforeseen circumstance occurs it should remain at about £1500 a year. The Reserve for Publications now stands at £2546, as shown on the next page.

Library Account.

The Account has a balance of £132 after paying the usual items. Our late Fellow, Mr. R. J. Flintoff, has left to the Library the sum of £1000, to be known as the Flintoff Bequest, for the purchase of books, which will be a great help to the Society.

Library Restoration Fund.

This fund has a balance of £1712. The Society has received during the year, £250 from the Royal Society and £57 from the Trustees of the Imperial Botanical Conference, 1935, and a further £54 has been received from Fellows. I am sure that all Fellows will be most grateful for these gifts to the Fund.

The binding and repairs to books is going well but there is still much to do. This expert work is very costly. The Library Committee are gradually purchasing the arrears of foreign works that are missing from our sets. There are liabilities of £280 spent on these which will come into the next year's accounts. I should like to appeal to all friends of the Linnean Library to help this Fund in any way they can, by donations or legacies, in order that this historic and valuable library can be maintained and conserved.

Trust and Reserve Funds.

I have already mentioned the Publications Reserve and the only other items that require explanation are the Reserve Fund to pay the balance of the cost of the Central Heating System, which has been completely renewed. We have now received the bill for this balance and after this payment the Reserve Fund will be expended. The £15 deposit of Dr. Uggla was left by him upon his return to Sweden in 1948. You will remember that Dr. Uggla visited the Society to compile the data for a Catalogue of the Linnaean Manuscripts, and the preparation of this Catalogue continues. Dr. Uggla is a leading authority on these Linnaean matters and I am sure we are all grateful to him for undertaking this task.

Under the Crisp Award you will see £148 Consol. Stock has been bought. Under the rules, if no award is made within 10 years, the interest must be invested and added to the Capital. The last award was in 1940.

Investments.

The holding of 2½% Consolidated Stock in the General Account has been increased by the investment of the Composition Fees received during the year.

The holding in the Library Account has been increased by the investment of the Flintoff Bequest in 2½% Consolidated Stock, and in the Special Accounts by the investment of the income of the Crisp Award, and Staff Pension Fund, in 2½% Consolidated Stock and 3% Savings Bonds respectively.

I should like to thank Mr. O'Grady, our Clerk, for the excellent manner in which the accounts have been kept. Mr. O'Grady carries out the detailed work in keeping the accounts and I am grateful to him for the conscientious way in which this work has been done.

If any Fellow wishes to ask any questions on these accounts, I will do my best to answer them.

[The Treasurer's Accounts are printed on pp. 242–245.]

On a motion by Dr. S. E. CHANDLER, O.B.E., seconded by Dr. HUGH SCOTT, F.R.S., the Report and Statement of Accounts were adopted.

The PRESIDENT then delivered his Address on ' The Heterocyst, a botanical enigma '.

On its conclusion, Mr. I. H. Burkill moved ' That the President be thanked for his excellent Address, and that he be requested to allow it to be printed and circulated amongst the Fellows '. The motion was seconded by Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S., and, being put to the meeting, was carried with acclamation.

The President announced that he appointed the following as the Vice-Presidents for 1950–51 :—Prof. G. D. Hale Carpenter, M.B.E., Mr. C. C. Hentschel, Mrs. Vera Higgins, V.M.H., and Colonel F. C. Stern, O.B.E., M.C.,

Thereafter the President declared the Session of 1949–50 closed.

PRESIDENTIAL ADDRESS

By Professor F. E. Fritsch, F.R.S., P.L.S.

The Heterocyst: A Botanical Enigma.

(With Plate 5* and 122 text-figures.)

It is, to say the least, very unusual to find in a circumscribed group of plants a structure exhibiting a considerable degree of specialization for which, in the present state of our knowledge, it is impossible to suggest a really plausible function. Yet this is true of the cells called heterocysts, which are found in the majority of the filamentous Blue-green Algae, the Myxophyceae or Cyanophyceae, as they are variously called. There is no very great degree of differentiation among the cells in most of the filamentous members of this class and, for example among the Nostocaceae, all the cells of the threads tend to be alike, apart from the heterocysts, the specialized end-cells of some species, and the cells which sooner or later develop into spores or, as they would better be called, akinetes.

It will be familiar that the cells of the Blue-green Algae have a protoplast which is differentiated into a peripheral region, the chromatoplasm, containing the photosynthetic pigments, and a colourless centroplasm which contains substances resembling chromatin and possibly fulfils some of the functions of a nucleus. I have no intention of discussing the many conflicting statements centering around this curious cellular organization, but it is necessary to draw attention to certain other peculiarities of the blue-green cell, Foremost among these are the firm gel-like character of the protoplast and the absence of obvious vacuoles. In a healthy blue-green cell the sap appears to be held by imbibition. The appearance of vacuoles is a herald of death and, as a general rule at least, the condition is irreversible.

Except in starved cells, more or less copious granules of various sizes are present, and they usually constitute a characteristic feature of the blue-green protoplast. The granules are of varied nature and require further study, but many of those that are lodged in the chromatoplasm consist of a nitrogenous substance called cyanophycin which is probably proteinaceous in character. The carbohydrate reserves of the blue-green cell are diffused through the protoplast and consist of a substance similar to glycogen which is itself possibly often combined with protein (*cf.* Baumgaertel, 1920, p. 97 ; Poljansky and Petruschewsky, 1929, p. 33). The reddish-brown coloration, which the protoplast assumes on treatment with iodine, is due to the content of glycogen.

The envelopes of the vegetative cells are differentiated into an inner and an outer region (Fritsch, 1905, p. 195). The inner portion (the inner investment)

* I am indebted to Mr. R. Cullen, Laboratory Steward, Department of Botany, Queen Mary College, for the photomicrographs on this plate.

completely surrounds the protoplast, but is not usually very sharply marked off from it; it appears in optical section as a comparatively thin colourless strip and, in filamentous forms, constitutes the septa between the individual cells (Mühldorf, 1937, p. 219; 1938, p. 17; 1938 a, p. 317). The outer portion (the cell-sheath) forms a barrel-shaped envelope, open at both ends, round each cell and, especially in the Nostocaceae, is often confined to the individual cell; it is clearly evident in material stained with iodine reagents. It may be a secretion of the protoplast or a differentiated outer layer of the inner investment, but its chemical nature is obscure. The inner investment is in very close contact with the protoplast and is itself probably but a modified outer layer of the latter, resembling the periplast of flagellates, although perhaps rather softer; in all probability it is in part at least composed of living substance. When blue-green cells are immersed in sufficiently strong hypertonic solutions, the protoplast shrinks irregularly, and the envelopes often contract with it or only separate from it at a few places.

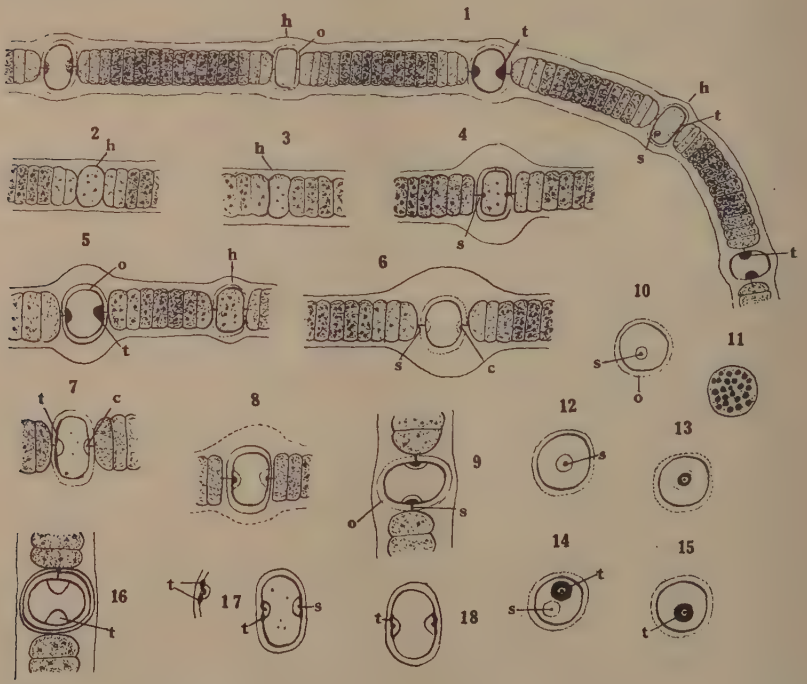
There are two kinds of heterocysts, spoken of respectively as terminal and intercalary and differing slightly in structure. Terminal heterocysts are situated at the termination of a length of thread (*cf.* figs. 49–67, 98, 99), whereas intercalary heterocysts are scattered, often at more or less equal intervals, among the other cells within the course of a thread (*cf.* fig. 1 and Pl. 5, A).

The accounts of heterocysts, usually given in descriptions of the group, suggest a degree of uniformity of structure and behaviour which does not altogether correspond with the facts. In figures of heterocystous blue-green algae these structures are usually shown as empty cells, for the most part rather wider than the other cells and with a firm clearly defined wall of moderate thickness, often rather thicker at the ends adjacent to vegetative cells. The impression thus given that these cells lose their contents at an early stage and sever connection with the adjoining cells, is conveyed in many accounts of the the class, but is far from being correct. As long as the threads are actively growing, intercalary heterocysts usually occur singly, are not very numerous and, as already stated, are often placed at more or less equal intervals (fig. 1). The condition sometimes found in nature and more frequently in cultures, in which series of heterocysts lie adjacent to one another, I believe as a general rule to be a symptom that the threads in question are reaching the end of their period of activity and are no longer in a normal condition.

It is probably the heterocysts of Nostocaceae that have most often been the subject of study, and I, too, have devoted most of my attention to them. Many members of that family afford suitable material, but the changes that occur during the development of the heterocysts are probably most easily followed in the species of *Nodularia*, although the general sequence is essentially the same in all the Nostocaceae and Rivulariaceae I have examined. The heterocyst invariably arises from a vegetative cell by a series of changes and, prior to the onset of spore-formation, most stages are to be met with in an actively growing thread of a *Nodularia*. The first stages are to be sought in the middle of the lengths of vegetative cells extending between two older (intercalary) heterocysts and are recognizable (figs. 1, 2, *h*) as single, often somewhat longer, cells with contents of a rather lighter shade and usually containing fewer granules; such incipient heterocysts are sometimes slightly biconcave (fig, 3 *h*) which seems to be a result of the rounding off of the contiguous faces of the cells on either side.

In the next stage (fig. 1, *h*) there is a slight spatial separation of the future heterocyst from the adjacent cells. This is due to the development around it of a hyaline and seemingly somewhat gelatinous envelope (*o*) which I believe arises, in part at least, through modification of the cell-sheath. As this spatial separation occurs, a delicate thread-like strand (figs. 1, 4, 6, *s*) remains between the protoplast of the heterocyst and that of the adjacent vegetative cell on

either side. According to Mühldorf (1937, p. 223) these strands consist only of the extended cell-membrane forming a tubular connection between heterocyst and vegetative cell and at most containing only remnants of protoplasm. The marked staining of these strands with cotton blue in lactophenol, up to late stages, however, leads me to conclude that there is, for some very considerable time at least, an actual cytoplasmic connection between the two protoplasts whereby protoplasmic continuity is maintained. The strands appear uniformly tinted throughout and do not give the impression of being hollow, while the septa between the vegetative cells and the immediate envelopes of the latter are scarcely affected by cotton blue.



FIGS. 1–18.—*Nodularia spumigena* Mertens. 1, part of a long thread, with immature heterocysts arising between mature ones. 2–8, parts of threads with heterocysts in various stages of development; 2, 3, first stage; 5 (on the right), second stage, with connecting strands and no thickening; 4, 8, third stage, button-like thickening; 6–8 show outline (*c*) of future thickened area; 5 (on the left), fourth stage, mature heterocyst. 9, 16–18, heterocysts on a larger scale, showing details. 10, 12–15, end-views of heterocysts; 10, 12, second stage; 13, third stage; 14, 15, fourth stage. 11, end-view of vegetative cell. *c*, area of future thickening of inner investment; *h*, young heterocyst; *o*, outer envelope of heterocyst; *s*, connecting strand; *t*, polar thickening of inner investment. (7–9, 11, 16–18 ×1000; the rest ×750.)

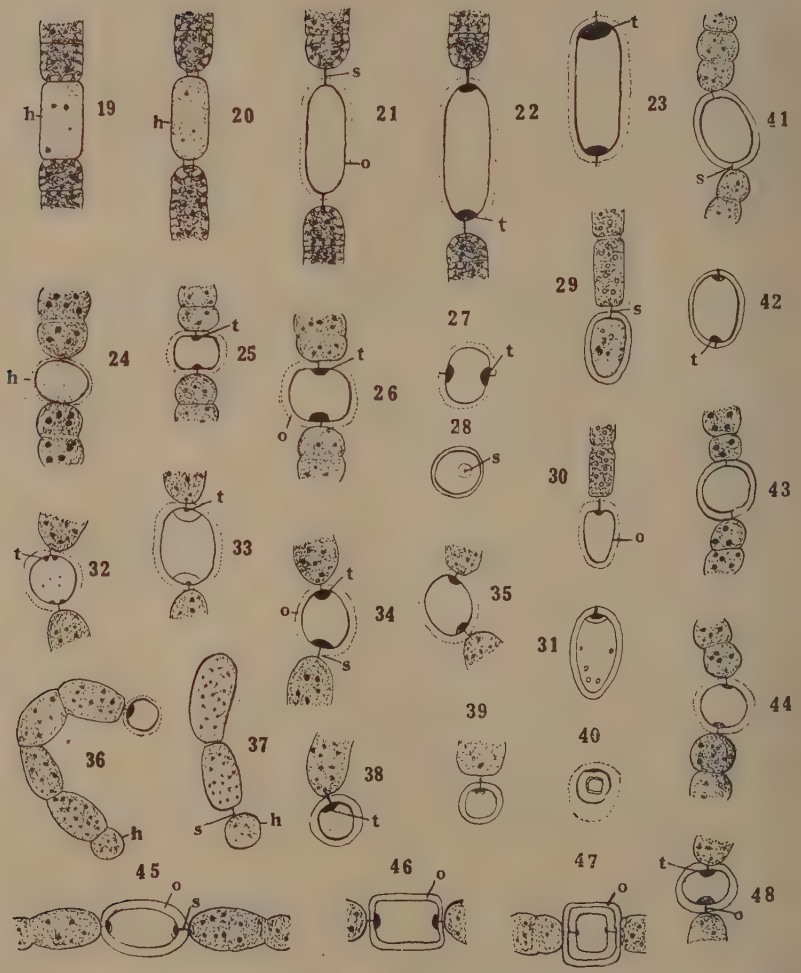
Up to this time the protoplast of the heterocyst which usually undergoes some further enlargement, especially in the transverse direction, is still supplied with a certain amount of granular matter (fig. 4), although both it and the adjoining cells on either side are often less granulate (figs. 1, 6) than the other vegetative cells. The next noticeable change takes place at the poles of the heterocyst, where the inner investment undergoes modification around the

points where the cytoplasmic strands just discussed connect with the protoplast of the heterocyst. This polar modification first becomes recognizable in optical section merely as a somewhat darker and apparently firmer strip of membrane (figs. 1, 82, *t*), which seems as a general rule to appear sooner at one pole than at the other ; sometimes the strip can be seen to be interrupted (fig. 7 ; *cf.* also figs. 17, 82, *t*) where the strand passes in. This strip no doubt represents the optical section of a more or less circular area of the inner investment—sometimes recognizable as a semicircular, more lightly stained, patch at a higher focus (figs. 6, 7, *c*)—where this envelope is undergoing slight thickening (*cf.* also Geitler, 1942, p. 23) and other changes around the point where the connecting strand links up with the protoplast (*cf.* also Pl. **5**, C–E).

By degrees this modified area becomes thicker and more evident and in cotton blue preparations deeply stained ; first it appears merely as a button-like thickening around the end of the connecting strand (figs. 4, 8, 9), but it may ultimately become very conspicuous and appear semi-elliptical or semicircular in shape (figs. 1, 5, *t*). On casual inspection it then looks rather like a large conical or hemispherical plug of material projecting into the interior of the heterocyst (*cf.* fig. 16), and such structures are commonly, though often rather diagrammatically, indicated in figures of blue-green algae. They may be responsible for the widespread references to the occurrence in heterocysts of marked polar thickenings and plugs. In the flat heterocysts of *Nodularia*, in particular, it is easy to convince oneself, however, that there are no very marked inward projections at the poles and that the conspicuous structures to be seen there are essentially surface modifications—albeit of some degree of thickness—of the membrane immediately surrounding the protoplast of the heterocyst.

Detached heterocysts of *Nodularia* and the spherical heterocysts of some species of *Anabaena* (*cf.* fig. 28) are readily viewed from the poles. In such aspects these specialized circular areas of the inner investment around the strands joining their protoplasts with those of the vegetative cells look like bordered pits, the connecting strand itself occupying the position of the pits (figs. 10, 12). All stages in the development of these areas can be seen in such polar views (figs. 12–15). The connecting strand is often detached with the heterocyst and then appears as a projecting stalk (*cf.* figs. 23 and 27). Even in heterocysts, still *in situ* in the threads of a *Nodularia*, a slight obliquity often causes one or other pole to present the appearance of a half-bordered pit (figs. 17, 18). Such a picture is also afforded by the heterocyst figured by Kohl (1903) on Tab. e, fig. 5.

These thickened areas at the poles, though varying in their degree of development, are very characteristic of the mature heterocyst. As already mentioned, they take on a very dark blue tint with cotton blue and, in this respect, resemble the larger cyanophycin granules found in some of the vegetative cells. The older accounts of heterocysts often speak of polar cyanophycin granules (*cf. e.g.* Geitler, 1936, p. 71), but although occasional granules resembling cyanophycin may persist here and there in a mature heterocyst (figs. 7, 17, 31, 32), I have not met with loose granules at the poles opposite the connecting strands. The polar structures of which I am speaking and which, in most Nostocaceae at least, are quite regular in their occurrence, are always part of the inner envelope immediately surrounding the protoplast, and a study of their development gives the impression that they are a modification of that envelope. The material of which they are composed may be chemically similar to cyanophycin, though probably not identical with it. Treatment of the threads with 35% chromic acid leads to a gradual solution of the cytoplasm and its contents so that at a certain stage only the envelopes of the ordinary vegetative cells and of the heterocysts persist; in the latter, however, the polar thickenings survive unaltered, when the cyanophycin granules of the vegetative cells have disappeared. Ultimately everything is dissolved.



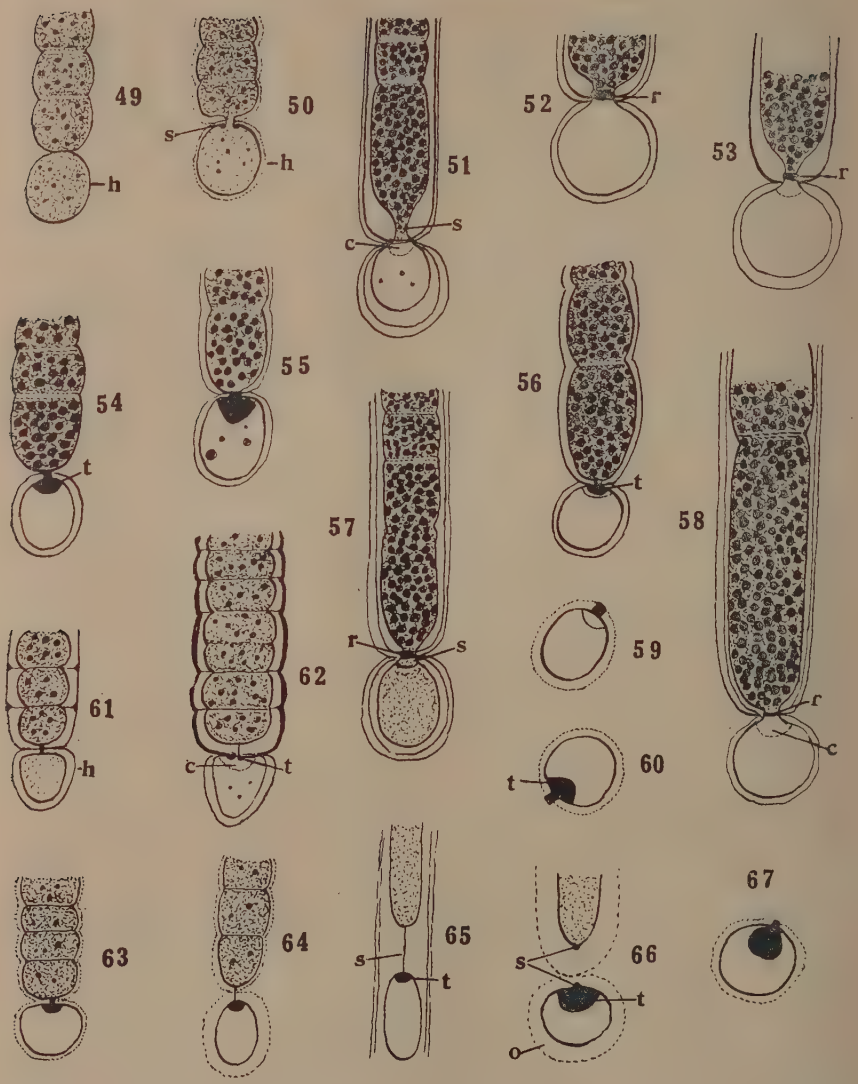
FIGS. 19–48.—Heterocysts of Nostocaceae. 19–23, *Aphanizomenon flos aquae* (L.) Ralfs, successive stages of heterocysts. 24–28, *Anabaena sphaerica* Born. et Flah.; 24–26, successive stages of heterocysts; 27, detached mature heterocyst; 28, end-view of young heterocyst. 29–31, *Cylindrospermum alatosporum* F. E. Fritsch, terminal heterocysts; 29, 30, two successive stages; 31, older detached heterocyst. 32–35, *Anabaena circinalis* (Kütz.) Hansg., successive stages of development of intercalary heterocysts. 36–40, *Anabaenopsis circularis* (G. S. West) Miller; 36, recently detached thread, with one mature and one young heterocyst (*h*); 37, heterocyst in second stage; 38, 39, older heterocysts; 40, ditto after treatment with iodine and sulphuric acid. 41, 42, *Nostoc verrucosum* Vauch.; 41, heterocyst *in situ*; 42, detached heterocyst. 43, 44, *N. coeruleum* Lyngb. 45–48, *Anabaena variabilis* Kütz. var. *ellipsospora* Fritsch, heterocysts of various ages; 47, after treatment with iodine and sulphuric acid. *h*, young heterocysts; *o*, outer envelope of heterocyst; *s*, connecting strand; *t*, polar thickening of inner investment. (29, 30 ×1000; 32–35, 41, 42 ×1250; the rest ×1200.)

The polar thickenings are no doubt chemically modified parts of the inner membrane of the heterocyst, but during their development the whole of the inner envelope acquires a better definition and probably undergoes some thickening. The outer part is readily and deeply stained by iodine reagents. The differentiation of this firm inner membrane around the contents of the heterocyst no doubt severs all communication between its protoplast and that of its neighbours, save by way of the cytoplasmic strands. These seem to be an essential equipment of the heterocyst in most of the Cyanophyceae I have examined, and the special polar thickenings may serve the purpose of strengthening this connection.

The sequence of stages so far described, most of which can be seen quite readily even in unstained material, can also be traced in the species of *Anabaena* I have examined (figs. 24–26, 32–35 ; *cf.* also figs. 19–23 and Pl. **5**, D, E of *Aphanizomenon flos aquae*). The only noteworthy difference is met with in heterocysts of the terminal type, which possess only one connecting strand developed on the side adjacent to a living vegetative cell (see figs. 29–31, 86–89, 92, Pl. **5**, B, I). The series of stages shown for the development of the terminal heterocysts of *Anabaenopsis* (figs. 36–39) illustrates without further words their identity in all other respects with those described for *Nodularia* (see also p. 204).

The outer envelope of the heterocyst, which like the inner is colourless, varies somewhat in texture, being either rather gelatinous (figs. 9, 10, 21, 26, **34**, *o*), though usually with a well-defined outer boundary, or appearing as a firm moderately thick membrane, traversed at one or both poles by a narrow pore through which the connecting strand passes (figs. 45–47, *o*) ; the edges of the pores may be slightly thickened. I suspect that the differences depend in part on whether there is a general mucilage-envelope to the thread or not, and in part on the age of the heterocyst. A part of this outer envelope sometimes consists of a substance which takes on a blue coloration with iodine and sulphuric acid or with chlor-zinc-iodide. The fact that the outer envelope of the heterocyst contains cellulose has been variously asserted as being a universal feature (Hegler 1901, p. 273 ; Klein 1915, p. 535) or as one which is often but not always realized (Brand 1903, p. 40 ; Gomont, 1888, p. 224 ; Kohl 1903, p. 132). In my experience a blue coloration with chlor-zinc-iodide is commonly not obtainable and, even with iodine and sulphuric acid, it is quite often not produced. Whether the coloration obtained actually indicates the presence of cellulose is perhaps open to some doubt, seeing that so often chlor-zinc-iodide fails to give any positive reaction, although the brown coloration of the contents of the heterocyst indicates that the reagent has penetrated. I have a suspicion that the responsible cell-wall ingredient is more a feature of the ageing than of the mature heterocyst. Staining with ruthenium red (0·2%) or aqueous methylene blue gives little indication of the presence of pectins.

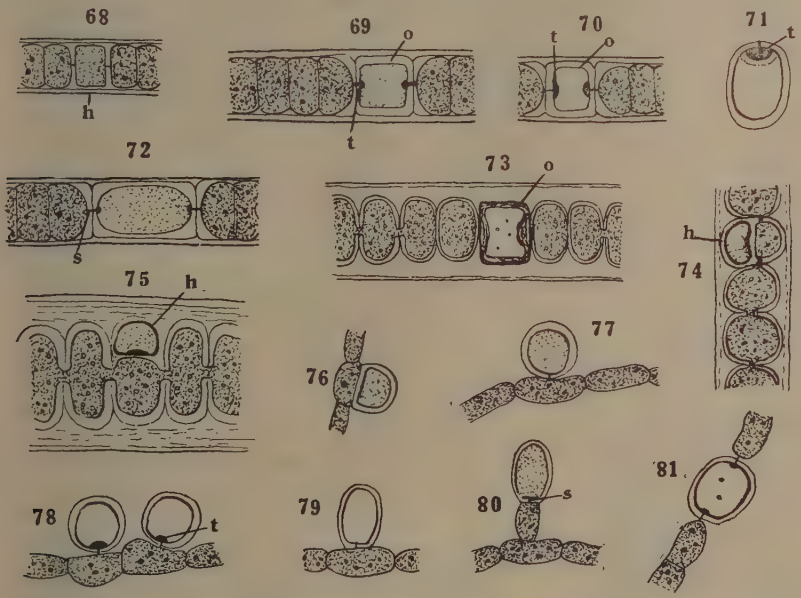
In the fully differentiated heterocyst the contents are usually quite clear and homogeneous, all the granules having disappeared. A somewhat similar change sometimes also affects the vegetative cells adjacent to intercalary heterocysts, as is specially apparent in *Nodularia* (figs. 1, 6). As a general rule there is no shrinkage of the contents of the heterocyst, even in later stages in threads in which differentiation of akinetes (spores) is almost complete. There is no reason to suppose that such heterocysts are dead or even moribund. The rather transparent appearance of their contents is probably the normal aspect of the blue-green protoplast when all granular matter has disappeared. The protoplast of the heterocyst often shows a yellowish coloration, which is due to disappearance of the photosynthetic pigments, leaving only the carotenes, a change known to take place readily in the blue-green protoplast as a result of nitrogen- and phosphorus-deficiency (Boresch, 1913 ; Maertens, 1914, p. 453 ; Pringsheim, 1913). It is, however, quite a misrepresentation to regard this change as an inevitable accompaniment of the differentiation of the heterocyst, since



FIGS. 49–67.—Heterocysts of Rivulariaceae. 49–60, *Gloeotrichia natans* (Hedw.) Rabenh, 49, first, 50, second, and 51–53, 58, third stages of heterocysts; in 52 and 53, stained with cotton blue, showing the ring (*r*) encircling the connecting strand; 54, 55, mature heterocysts; 56, about stage 3; 57, oblong heterocyst, with ring around connecting strand and young akinete; 59, 60, detached heterocysts. 61, 62, *Calothrix braunii* Born. et Flah., in 61 with young, in 62 with older heterocysts. 63–67, *Dichothrix compacta* (Ag.) Born. et Flah.; 63, 64, heterocysts *in situ*; 65, with drawn out connecting strand; 66, with the latter snapped; 67, detached heterocyst. *c*, area of future thickening of inner investment; *h*, young heterocysts; *o*, outer envelope; *r*, ring around connecting strand *s*; *t*, polar thickening. (52, 53 ×1000; 63–66 ×1600; the rest ×800.)

heterocysts, especially those of Nostocaceae and Rivulariaceae, not uncommonly retain a vivid blue-green colour up to the time of their death, a condition which seems especially common in tropical members of the Cyanophyceae. Nor does the frequent yellowing of the contents of the heterocyst imply a cessation of functions other than that of photosynthesis, and it is known that the normal pigments sometimes reappear.

I hope the description I have just given will have shown that heterocysts are highly specialized as compared with the ordinary blue-green cells, while the change in the contents of the protoplast, the not infrequent secretion of a special cellulose-like substance in the outer envelope, and the probable



FIGS. 68–81.—Heterocysts of Scytonemataceae and Stigonematales. 68–70, 72, *Scytonema hofmanni* Ag., intercalary heterocysts; 68, stage 2; 69, 72, stage 3. 71, *Tolypothrix tenuis* Kütz., mature terminal heterocyst. 73, 75, *Stigonema ocellatum* (Dillw.) Thur. var. *braunii* (Kütz.) Hieron.; 73, intercalary and 75, lateral (terminal) heterocysts. 74, *S. hormoides* (Kütz.) Born. et Flah. var. *africana* Fritsch, with a terminal heterocyst. 76–81, *Nostochopsis lobatus* Wood, forma; 76–80, various forms of lateral (terminal) heterocysts, in 78 almost mature; 81, intercalary heterocyst. *h*, young heterocysts; *o*, outer envelope; *s*, connecting strand; *t*, polar thickening. (68–72 ×1300; 73–75 ×875; 76–81 ×950.)

maintenance of cytoplasmic continuity with the adjacent cell or cells suggests marked chemical activity and a specialized metabolism. I have already referred to various respects in which heterocysts may differ among one another, such as the pigmentation of the contents, the character of the outer envelope, and the extent of the presence of a cellulose-like compound. In some species of *Nostoc* the polar thickenings seem rarely to differentiate properly before the heterocyst loses its connection with adjacent cells (figs. 41–44). In the present state of our knowledge it is impossible to say how far the various differences referred to depend on environmental factors or are actual specific differences.

Another respect in which heterocysts of Nostocaceae differ among one another lies in the readiness with which they separate from the adjacent cells

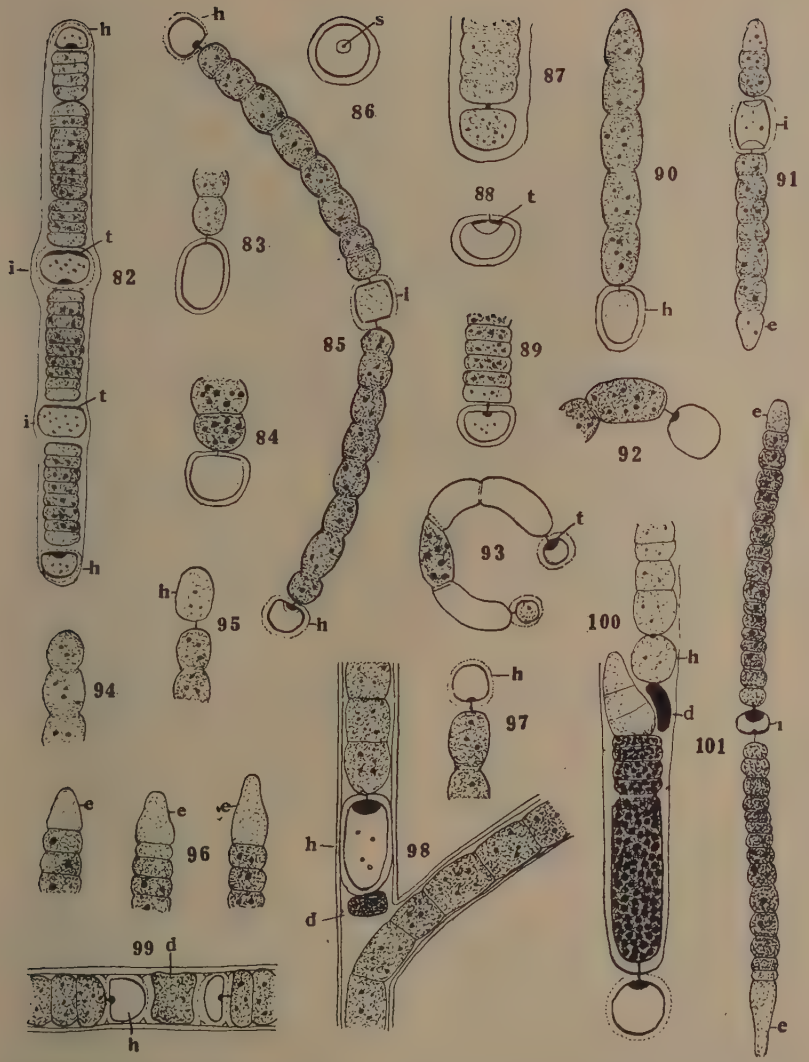
on attaining maturity. In many species of *Nostoc* and in some Anabaenas this occurs so easily that, especially in the former, it is often difficult to find a heterocyst *in situ* in a mature colony (Pl. **5**, J).

Among the few Rivulariaceae I have examined, where the heterocysts are nearly always of the terminal type, those of *Calothrix* show much the same features (figs. 61, 62 and Pl. **5**, G) as in the Nostocaceae. In *Dichothrix* (figs. 63–67) they tend to form successively at the bases of the threads, usually lose their connection with the overlying cells at an early stage and sometimes fail to develop polar thickenings ; there is here some analogy with the behaviour of the (intercalary) heterocysts of *Nostoc*. The older heterocysts are often widely separated from the thread to which they belong, the connecting strand being either markedly extended (fig. 65, *s*) or, more usually, broken across, one part adhering to the lowest vegetative cell, the other to the displaced heterocyst (fig. 66, *s*). The spherical heterocysts of *Gloeotrichia natans* (figs. 49–60) are connected with the overlying vegetative cell by a particularly coarse strand (figs. 51–55, Pl. **5**, K, M) which commonly exhibits an encircling ring, staining deeply with cotton blue (figs. 52, 53, 57, 58, *r* and Pl. **5**, K) ; in older heterocysts, such as are commonly found beneath developing akinetes, this ring seemingly widens and becomes continuous with the polar thickening of the inner investment (fig. 60).

I have not studied many representatives of the remaining heterocystous families, but so far as my observations go they are often distinguished by comparative paucity of heterocysts, at least in vigorously growing filaments. The intercalary heterocysts in such material of *Scytonema Hofmanni* and other species of the genus show all the typical stages in development (figs. 68–70, 72). As in other Scytonemataceae, the outer envelope (*o*) is joined to the sheath. Its inner part often stains blue with chlor-zinc-iodide, but much more markedly so in the older heterocyst. In *S. Hofmanni* a blue coloration was also evident in the membrane of the occasional dead cells present in the threads. Older material of diverse other Scytonemataceae that I examined showed heterocysts with comparatively thick walls and no recognizable connecting strands.

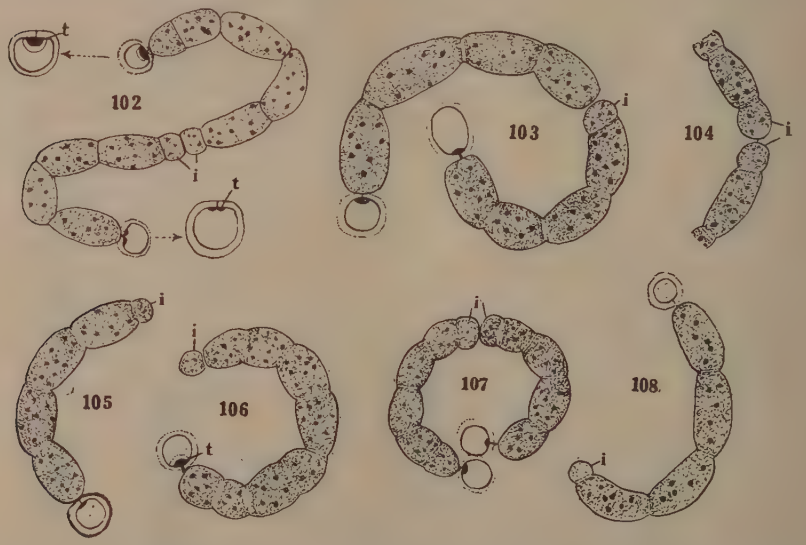
Such heterocysts are also found in *Stigonema* and other Stigonemataceae, where the many published figures afford no indications of connecting strands or even of pores at the poles and suggest that heterocysts are often few and far between. These features are specially evident in the species of *Stigonema* I have examined (*cf.* figs. 73–75), while repeated investigation of material of *S. ocellatum* from the New Forest has failed to disclose any structures that could justifiably be called heterocysts (Pl. **5**, N). Of the numerous other Stigonematales, I have examined only a species of the somewhat aberrant genus *Nostochopsis* where the heterocysts exhibit all the typical features (figs. 76–81 ; *cf.* also Desikachary, 1947, p. 226). The published figures of species of *Hapalosiphon* indicate that their heterocysts also approximate to the usual pattern, but a detailed comparative study of the heterocysts of Stigonematales is necessary in order to determine how far the structures so called correspond to those in Nostocaceae and Rivulariaceae. Both in Scytonemataceae and in Stigonemataceae I have the impression that the heterocysts in general exhibit shrinkage and death of their contents much sooner than is the rule in the other two families.

It will be useful at this stage of our considerations to deal with the distribution of terminal heterocysts. In many Nostocaceae (*Nostoc, Anabaena, Nodularia*) the threads that arise from germinating akinetes, at a relatively early stage, differentiate a terminal heterocyst at one or both ends (figs. 82, 85, *h*). Though very frequent, this is not an invariable phenomenon. The stretch of cells between the two terminal heterocysts may remain purely vegetative for a considerable length of time, but in most members of the family it is sooner or later interrupted by the development of an intercalary heterocyst, usually at



FIGS. 82–101.—Terminal heterocysts, etc. 82, 86–89, *Nodularia spumigena* Mertens; 82, thread with 2 terminal and 2 immature intercalary heterocysts; 86, terminal heterocyst in end-view, stage 3; 87, terminal heterocyst, stage 2; 88, 89, ditto, stage 3. 83, *Nostoc verrucosum* Vauch., and 84, *N. coeruleum* Lyngb., terminal heterocysts. 85, 90, 94, 95, 97, *Anabaena variabilis* Kütz. var. *ellipsospora* Fritsch; 85, germling with 2 terminal and a developing intercalary heterocyst (stage 2); 90, younger germling with a single terminal heterocyst (stage 2); 94, apex of thread, with undifferentiated end-cell; 95, young terminal heterocyst (stage 2); 97, older ditto (stage 3). 91, *A. sphaerica* Born. et Flah., germling with intercalary heterocyst. 92, *A. circinalis* (Kütz.) Hansg., terminal heterocyst (stage 3). 93, *Anabaenopsis circularis* (G. S. West) Miller, thread with one mature and one young terminal heterocyst. 96, 101, *A. torulosa* (Carm.) Lagerh. forma; 96, end-cells of threads; 101, germling with differentiated end-cells and an intercalary heterocyst. 98, *Tolypothrix tenuis* Kütz., false branching. 99, *Scytonema hofmanni* Ag., formation of terminal heterocysts on either side of a dead cell (*d*). 100, *Gloeotrichia natans* (Hedw.) Rabenh., false branching. *e*, end-cells; *h*, terminal and *i*, intercalary heterocysts; *s*, connecting strand; *t*, polar thickening. (82, 86–89, 91, 93, 101 ×875; 83, 92, 99 ×1400; 100 ×700; the rest ×1250.)

approximately the middle of the thread (figs. 82, 85, *i*). After a further period of division other intercalary heterocysts appear consecutively in the course of the lengths of thread on either side of the first-formed one (figs. 1, 82). The frequency of such intercalary heterocyst-formation varies greatly in the species of *Anabaena*, while in *Nodularia* they always arise at frequent and rather regular intervals (Pl. 5, A, F). It is not known whether, when threads belonging to species of these genera fragment, as they commonly do after reaching a certain length, the end-cells of the daughter-threads remain vegetative or become converted into terminal heterocysts. The latter are, however, occasionally found developing from the cells on either side of an intercalary heterocyst so that the portions of threads thus separated will have a terminal heterocyst at least at one end (*cf.* fig. 99).



Figs. 102–108. *Anabaenopsis circularis* (G. S. West) Miller. 102, 107, Mature threads with incipient heterocysts; the terminal heterocysts in 102 shown enlarged. 103, terminal heterocysts of different shapes. 104, young heterocysts, with a connecting strand. 105, 108, recently fragmented threads, with young terminal heterocysts; in 108 the other heterocyst still in stage 2. 106, somewhat older stage. *i*, young heterocysts; *t*, polar thickening (×1200).

In one member of Nostocaceae, *Cylindrospermum*, intercalary heterocysts are only quite exceptionally formed and the threads retain throughout life the terminal heterocysts of the germling (fig. 110), although sometimes further terminal heterocysts develop successively from the cells adjacent to the first-formed one. The length of vegetative thread between the terminal heterocysts may be considerable (fig. 110), a fact to which I shall refer again in a moment. In another genus of Nostocaceae, *Anabaenopsis*, however, where terminal heterocysts likewise predominate, the threads subtended by them are much shorter. The usually coiled filaments here rarely consist of more than about 12–20 cells and, as soon as they reach a certain length, fragment into two.

In the material of *Anabaenopsis circularis* I have studied, such vegetative reproduction nearly always occurs when the threads consist of eight vegetative cells, although some of the eight cells are sometimes in process of subdivision. When the eight-celled stage has been reached, the two central cells (*i.e.* the fourth from either terminal heterocyst) divide unequally, so that pairs of small

contiguous cells are produced (figs. 102, 104, 107, *i*; Pl. **5**, H). These small cells are incipient heterocysts, and it is between them that rupture of the thread takes place. Each daughter-thread has at one end an older heterocyst and, at the other, one of these small cells (figs. 105, 106). At first it differs only in its size from the other four vegetative cells of the thread, but gradually it passes through the various stages (figs. 36–38, 93) previously described as occurring in the development of the nostocaceous heterocyst so that by the time that the new threads have become eight-celled they commonly again have a mature heterocyst at each end (figs. 102, 103). Judging by the figure given by Taylor (1932, pl. 39, fig. 9), it occasionally happens that no rupture occurs for a time at the point of heterocyst formation*, but I did not meet with such stages in my material.

The special relation between fragmentation and heterocyst-formation in *Anabaenopsis* helps to provide some data as to the sequence of the stages in the production of the heterocysts and the rate at which they are accomplished. As the table below shows, the new heterocysts rarely develop obvious polar thickenings (stage *c*) until the separated threads have reached the 7-celled stage, and it is only the 8-celled threads that show any considerable percentage with strongly developed polar caps (stage *d*, *cf.* fig. 103). Quite a large proportion of the 8-celled threads still possess, at one end, a heterocyst without evident thickening of the inner investment (stage *b*, fig. 106). On the other hand, in threads in which a new pair of heterocysts are being cut off, those at the two ends are both nearly always provided with marked polar thickenings (*cf.* figs. 102, 107). In the relatively rare instances in which this is not so, one part of the fragmented thread will have an immature heterocyst at each end (*cf.* fig. 108).

STAGES IN HETEROCYST-FORMATION IN ANABAENOPSIS (PERCENTAGES).

No. of cells in thread	*a*	*b*	*c*	*d*	Total threads counted
4	71	29	—	—	97
5	30	68	2	—	96
6	13	83	4	—	83
7	4	75	15	6	85
8	2	41	30	27	113
8 (with incipient heterocysts)	—	5	43	52	102

a, heterocyst undifferentiated (as in fig. 105); *b*, heterocyst separated from adjacent cell and with connecting strand (as in fig. 108); *c*, heterocyst with slight polar thickening (as in fig. 107); *d*, heterocyst with pronounced polar thickening (as in fig. 103).

The long threads of *Cylindrospermum* ultimately as a general rule fragment into two, but there is here no preliminary differentiation of heterocysts at the place of fragmentation, and there seems to be no clear evidence that the vegetative end-cells of the fragmented thread can give rise to a new heterocyst at all, although this may well be possible.

The threads of Nostocaceae are therefore very commonly, at least in their early stages, subtended by terminal heterocysts, while in *Cylindrospermum* and *Anabaenopsis* this juvenile condition persists throughout life and the

* In another species (*A. arnoldii* Aptek.) Aptekarj (1926; *cf.* also Geitler, 1936, p. 71) shows the same feature and depicts several pairs of intercalary heterocysts in the middle of a thread. This is, so far as I know, the only species of *Anabaenopsis* in which intercalary heterocysts are recorded. Ramanathan (1938), in describing an Indian form of *A. arnoldii*, likewise shows paired intercalary heterocysts, but states that, when, after fragmentation, the heterocysts come to occupy the ends of the threads, one polar thickening is far less conspicuous than the other. Taylor (1932) only shows true terminal heterocysts in the forms of this species which he describes. I very occasionally observed a connecting strand between the two incipient heterocysts (fig. 104). The matter merits further enquiry.

terminal are not supplemented by intercalary heterocysts. Exceptions to the prevalent occurrence of terminal heterocysts on the young threads are met with, *inter alia*, in certain species of *Anabaena* and probably also in some Nodularias. In the Anabaenas in question the end-cells of the young threads are usually more or less clearly differentiated from the others. They are frequently conical, with a more or less obtuse apex (figs. 91, 101, *e*) ; sometimes they are appreciably longer than the other cells and attenuated (fig. 96, *e*), and usually they contain far less granular matter. They often exhibit some decrease in the photosynthetic pigments and seem incapable of further division. Both in these respects and in the nature of their contents there is a suggestion of homology with heterocysts. In an Indian variety of *Anabaena variabilis* (var. *ellipsospora*) that I have recently studied (Fritsch, 1949, p. 142) the terminal cells of the threads show all gradations between normal vegetative cells (fig. 94) and typical terminal heterocysts with connecting strand and polar thickening (figs. 95, 97). By contrast in material of *A. torulosa*, from the same habitat, I could find no terminal heterocysts, although the end-cells were in part of a very distinctive pattern (fig. 96, *e*). May it not be that the specialized end-cells represent heterocysts which have not passed beyond the first stage in their differentiation and, although showing changes in contents and pigmentation, betray none of the other typical characteristics of heterocysts? The conditions determining formation or non-formation of terminal heterocysts in Nostocaceae might prove a fruitful subject for experimental study.

Whether or not it should prove possible to induce the formation of terminal heterocysts in a species that does not usually produce them, their widespread occurrence in Nostocaceae is significant. Not only do *Cylindrospermum* and *Anabaenopsis* almost only possess this type, but in species of *Anabaena* (figs. 92, 97), *Nodularia* and *Nostoc* (figs. 83, 84) they are often present in germlings and differentiate before any intercalary heterocysts are formed. In fact *Aphanizomenon* is the only common genus of the family that seems completely to lack terminal heterocysts.

Terminal heterocysts are also the rule in the Rivulariaceae (figs. 49–67) and in many members of that family their presence at the base of the threads seems to be obligate. This is evident during the multiplication of the threads in a colony of *Rivularia* (Kohl, 1903, p. 130) or *Gloeotrichia*. The process (fig. 100) is initiated by the death of an intercalary cell (*d*) after which the lower moiety of the original thread continues its growth, later thrusting the upper to one side, while the latter develops a new terminal heterocyst (*h*) from its lowest cell and constitutes an independent thread. In the two genera mentioned copious mucilage-formation soon leads to the separation of the two threads, but in *Calothrix* these so-called false branches may remain for a time cohering. Intercalary heterocysts are not often met with in Rivulariaceae, although occasionally seen in some species of *Calothrix*.

By contrast to their frequency in Rivulariaceae and Nostocaceae, terminal heterocysts are scantily represented among Scytonemataceae where these structures are most commonly of the intercalary type (figs. 70, 72). It is, however, significant that, when single false branches are formed in a *Tolypothrix* (fig. 98), the cell beyond the point of rupture of the main thread, as in a member of Rivulariaceae, always develops into a terminal heterocyst (*h*). In most members of the two families it is seemingly essential for a terminal heterocyst to occupy the base of a thread, although in both there are genera (*Homoeothrix* among Rivulariaceae, *Plectonema* among Scytonemataceae) which lack all heterocysts and where branching, involving the exposure of the end of a new thread, occurs without heterocyst-formation.

Even among Nostocaceae heterocysts are sometimes lacking. In the common planktonic *Aphanizomenon flos aquae* the threads are at times altogether devoid of them and such a condition is also known to occur occasionally in *Anabaena*. I have recently described a species (*A. naviculoides*), raised in

culture from the mud of Indian rice-fields, in which the elongate moniliform threads only rarely harbour a heterocyst, so that most of them would be referred to the doubtful genus *Isocystis*. A genus *Pseudanabaena* was established by Lauterborn (1916, p. 437) for blue-green algae with unbranched threads, consisting of barrel-shaped cells like those often composing the threads of *Anabaena*, but quite devoid of heterocysts. In one species of this genus (*P. constricta* (Szafer) Lauterb.) heterocysts have since been reported (Koppe, 1924, p. 642), and it is not improbable that all the few species of *Pseudanabaena* are really Anabaenas in which heterocysts are suppressed under the conditions normally obtaining in their habitats.

Cannabaeus (1929, p. 7) found that, in cultures of *Anabaena variabilis* containing 0·2% sodium chloride, the number of heterocysts in the threads was nearly three times as great as in cultures lacking the salt. Her description does not indicate what proportion of the heterocysts in the culture with sodium chloride were in a healthy condition, and it is possible that the effect is pathological, since excessive production of heterocysts is usually associated with material that is senescent and no longer growing satisfactorily.

Fogg (1944) finds that the frequency of heterocysts in *A. cylindrica* is inversely related to the concentration of combined nitrogen in the threads, and later (1949, p. 258) he suggests that their formation may be inhibited by increasing concentrations of a specific nitrogenous compound or compounds within the alga. When nitrogen is supplied in the form of ammonium salts in the culture medium, heterocyst-formation is, according to him (1949, pp. 243, 258), markedly inhibited as long as appreciable quantities of it remain in the medium. He suggests that arrest of heterocyst-formation in the presence of ammoniacal nitrogen may be a widespread phenomenon in the heterocystous blue-green algae, since *Gloeotrichia natans*, growing in an impure culture with ammonium chloride, showed complete absence of heterocysts, although these were present in the usual position in similar cultures without the ammonium salt. It is significant in this connection that Lauterborn's *Pseudanabaena* inhabits putrefying bottom-deposits where presumably ammoniacal nitrogen predominates. Fogg also established that certain conditions lead to an increase of heterocysts, but lack of time does not permit me further to consider these interesting results. Their value would be enhanced if some details were given of the state of the heterocysts in the various cultures.

The existence in nature of certain nostocaceous forms in which heterocysts are ordinarily lacking or only very rarely produced, combined with Fogg's data, suggests an enquiry into the status of *Plectonema* and *Homoeothrix*, with their close approximation in all other respects to *Scytonema* and *Calothrix*. Both in *Scytonema* and *Tolypothrix* the heterocysts are often few in number, and it may be that factors may be found that cause their complete elimination or, alternatively, call forth heterocyst-production in *Plectonema*.

When the protoplast of an intercalary heterocyst dies, all connection with the adjacent cells on either side is severed so that fragmentation of the thread occurs at this point. In *Nostoc*, *Nodularia*, and many species of *Anabaena*, frequent vegetative reproduction ensues in this way, and it is not surprising that this has by some been regarded as a main function of the heterocyst. Quite apart from the fact that it is absurd to suppose that such a highly differentiated structure should be produced solely for the purpose of bringing about fragmentation of the threads, similar fragmentation occurs by modification and death of occasional intercalary cells in many non-heterocystous genera and, even in the heterocystous forms, is by no means only effected with the help of heterocysts. We can therefore regard the part which heterocysts play in fragmentation as quite irrelevant to their main function and as one that can be fulfilled by many other cells of the blue-green filament.

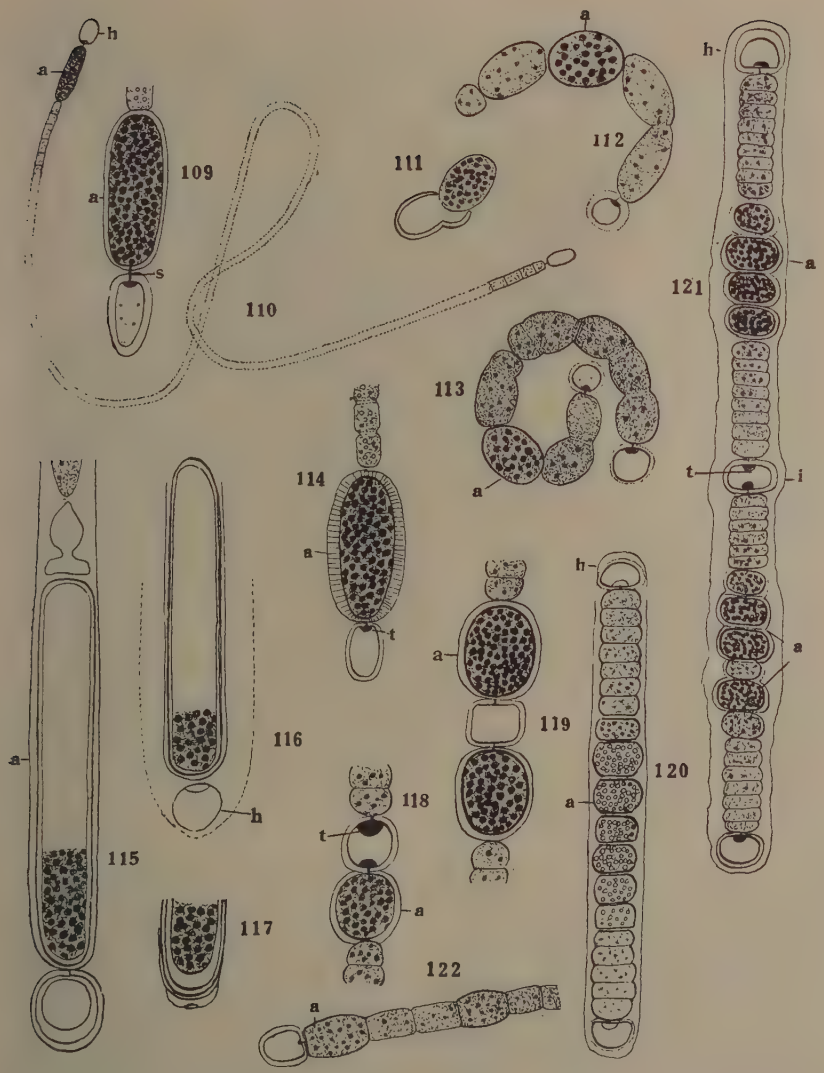
In quite a number of genera occasional germination of the contents of a heterocyst has been observed (Geitler, 1921 ; Geitler, 1936, p. 75 ; Hollerbach,

1928; Steinecke, 1932; Desikachary, 1946). It is unnecessary to consider the detailed data which have led to the formulation of the theory that heterocysts are archaic reproductive cells or spores, nowadays largely functionless, although exceptionally reverting to their original function (Geitler, 1921). It must be realized that such rejuvenescence of the contents is extremely rare. I have during the past six months examined a large quantity of material belonging to diverse heterocystous genera and coming from all parts of the world without seeing a single instance of such germination. It must be concluded therefore that, when it occurs, the protoplast of the heterocyst has merely recovered the capacity for growth and division which it normally loses during its differentiation. Many heterocystous genera, especially among Nostocaceae, reproduce copiously by means of akinetes (spores), and it would indeed be strange if there were two kinds of such reproductive units, the one largely functionless.

Cannabaeus (1929), because of certain alterations (increases or decreases) in the size of the heterocysts of species of *Anabaena*, when grown in culture media containing an alkaline or metallic salt, propounded the view that these structures were enzyme-receptacles, although no evidence for the presence of any enzyme was produced. It was further suggested that the enzyme or enzymes involved were responsible for the formation of the so-called gas-vacuoles (pseudo-vacuoles) in the vegetative cells of diverse heterocystous Nostocaceae that commonly produce water-flowers. There are, however, blue-green algae possessing such gas-vacuoles and occurring abundantly in the plankton, which lack heterocysts, while *Aphanizomenon flos aquae*, one of the commonest of the Nostocaceae to occur as a water-flower, as already mentioned, at times possesses no heterocysts. Cannabaeus' hypothesis is in fact so ill-founded that I should not have mentioned it at all, were it not that it was the first to ascribe a vital function to the protoplast of the heterocyst. I suspect that it contains a core of truth in the suggestion that this activity consists in the secretion of a substance or substances that are passed on to other cells.

It is a striking fact that heterocysts, which long retain an unshrunken, even though transparent, protoplast occur for the most part in genera of Nostocaceae and Rivulariaceae in which akinete-(spore-)formation is a frequent, if not an invariable, feature of the mature threads. Many authorities have already commented on the relative positions of akinetes and heterocysts in these genera. When only terminal heterocysts are present, as in *Cylindrospermum* and *Gloeotrichia*, the akinetes, with very rare exceptions, develop next to them, are usually produced singly, and are of large dimensions (figs. 109, 114, 115, *a*; Pl. 5, B, K). The subterminal position of the akinetes in the often elongate threads of *Cylindrospermum* (fig. 110) is especially striking and suggests that, in the absence of other than terminal heterocysts, akinete-formation cannot take place elsewhere. It is conceivable that *Cylindrospermum* presents us with the primitive condition which has persisted in all the spore-forming Rivulariaceae.

In the other Nostocaceae, akinetes arise at intervals along the length of a thread, and none are usually produced next to the terminal heterocysts when these are present. In an Indian species (*A. oryzae*) I have, however, occasionally observed akinete-formation taking place in this position (fig. 122, *a*) and no doubt other examples of the same kind could be found. As a general rule the akinetes in Nostocaceae either develop next to or between successive intercalary heterocysts. When the former is the case, the akinetes (figs. 118, 119, *a*) are frequently in ones or twos, on one or both sides of the heterocyst, whilst when they are formed between two intercalary heterocysts they not uncommonly occur in shorter or longer series (figs. 120, 121, *a*; *cf.* also Geitler, 1936, p. 74). The latter condition is strikingly realized in *Nodularia*, which often possesses long threads of several hundred cells, with heterocysts at almost equal intervals and akinetes developing centrifugally from about the middle of each length of vegetative thread (Pl. 5, C, F). The akinete first formed is often larger



FIGS. 109–122. Heterocysts and akinetes (spores). 109, 110, 114, *Cylindrospermum alatosporum* Fritsch; 109, young and 114, mature akinetes next to terminal heterocysts; 110, entire thread with a heterocyst at each end. 111–113, *Anabaenopsis circularis* (G. S. West) Miller; 111, germinating akinete; 112, 113, threads with akinetes. 115–117, *Gloeotrichia natans* (Hedw.) Rabenh.; 115, 116, bases of threads with ripe akinetes; 117, basal part of akinete, after detachment of heterocyst. 118, 119, *Anabaena sphaerica* Born. et Flah., with ripe akinetes adjacent to intercalary heterocysts. 120, 121, *Nodularia spumigena* Mertens; 120, formation of akinetes in a germling; 121, ditto in older germling. 122, *A. oryzae* Fritsch, young akinete next to terminal heterocyst. *a*, akinetes; *h*, terminal and *i*, intercalary heterocysts; *s*, connecting strand; *t*, polar thickening. (110 ×400; 109, 114, 120, 121 ×850; 111–113, 122 ×1200; 115–117 ×700; 118, 119 ×1000.)

than those produced later (fig. 121). As already mentioned, the cells adjacent to the heterocysts in such sporogenous threads often contain very little granular matter and in this respect contrast very markedly with the akinetes, which are densely filled with large and conspicuous granules. One obtains an impression of regions adjoining heterocysts where there is a depletion of reserves and of spore-forming regions where they accumulate in quantity.

Akinete-formation can, however, take place in young threads of *Nodularia* which possess only terminal heterocysts (fig. 120) and such a condition, which is the antithesis to that found in *Cylindrospermum*, is also met with in *Anabaenopsis*. Here (figs. 112, 113) akinetes (*a*) most usually develop singly from the third cell from the end, that is to say from the one adjoining that from which an embryo heterocyst is cut off (*cf.* also Pl. 5, I), although sometimes they may originate actually from the fourth cell. It is noteworthy that, both in *Nodularia* and *Anabaenopsis*, the akinetes commence to develop in the proximity of regions where at other times there is an urge to form heterocysts. Although this fact is specially manifest in these two genera, the same relation is traceable in some Anabaenas.

The origin both of intercalary heterocysts and of akinetes is associated with cessation of vegetative division and more or less marked enlargement, but whereas the formation of a heterocyst is accompanied by depletion of solid reserves, that of an akinete is accompanied by great accumulation of such reserves. There must, therefore, be a radical change when, in a region that would normally give rise to an intercalary heterocyst, akinete-formation ensues.

As a working hypothesis it may be suggested that heterocysts during the vegetative period secrete substances that stimulate growth and cell-division and, when the concentration of these substances falls off as the cells come to lie further and further away from heterocysts, production of other heterocysts is induced. When the reproductive period sets in, the nature of the secretion from the heterocysts changes, and something is formed that stimulates akinete-formation ; or perhaps there is merely an alteration in the reaction of the contents of the cells involved. It may be postulated that primarily, when only terminal heterocysts were present, their secretion in the reproductive phase resulted in the development of akinetes in their immediate vicinity. When intercalary heterocysts also appeared, akinete-production was still confined to their immediate neighbourhood, but larger numbers could be formed, as there were many centres instead of only two. Finally, akinete-formation, like intercalary heterocyst-formation, became induced at a distance from the centres from which the supposed substances stimulating akinete-production originated.

Most Nostocaceae that normally form akinetes from cells next to heterocysts rarely depart from this habit. On the other hand, when the akinetes are produced in series between the heterocysts, one occasionally finds one located next to a heterocyst. Despite such exceptions, the contrast between the two situations of the akinetes is as a general rule marked and may be employed with discretion as a valuable taxonomic character.

As a general rule, there is no outward change in the heterocyst during akinete-formation. In maturing sporogenous threads the heterocysts usually show marked polar thickenings (*cf.* figs. 109, 113, 114, 118, 121) and these seem ordinarily to persist even after dissociation of the threads. In *Gloeotrichia natans*, however, the detached heterocysts found beneath mature akinetes (fig. 116, *h*) lack all such thickenings.

In conclusion it may be well to recapitulate the essential facts. The widespread occurrence of terminal heterocysts in Nostocaceae and Rivulariaceae, both in young and adult stages, taken in conjunction with their specialized structure, indicates that they must fulfil a significant function. In most Nostocaceae, as the germlings increase in length by the division of their cells, other centres of a similar kind clearly become necessary, and intercalary

Heterocysts in Blue-green Algae.

heterocysts, with connections in both directions, are differentiated, often at approximately equal intervals within the threads. Similar intercalary heterocysts occur in Scytonemataceae where no formation of akinetes takes place. This suggests that the primary function of the heterocyst is concerned with growth and cell-division. In those blue-green algae in which akinetes are formed, a relation to living heterocysts is often very apparent and akinetes commonly arise from cells contiguous to these structures.

The concept of the secretion of a substance or substances by the heterocyst which stimulate the series of changes (enlargement, accumulation of food-reserves, modification of the membrane), that lead to the formation of akinetes, is easily acceptable in such instances, but it is not easy to understand why akinetes are not always produced in this position. The theory I have propounded on the basis of these studies of the structure and distribution of heterocysts may therefore prove to be another of the diverse untenable hypotheses put forward in the past and, if that be so, the heterocyst will remain as hitherto a botanical enigma.

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Explanation of the Plate

Plate 5.

A, *C*, *F*, *Nodularia spumigena* Mertens; *A*, vegetative thread, with 5 heterocysts; *C*, length of thread with two heterocysts, the upper mature, the lower in stage 2, and two series of akinetes; *F*, longer stretch of same thread on a smaller scale. *B*, *Cylindrospermum alatosporum* Fritsch, with a terminal heterocyst and an immature akinete. *D*. *E*. *Aphanizomenon flos aquae* (L.) Ralfs, heterocysts. *G*, *Calothrix braunii* Born. et Flah., threads with heterocysts. *H*, *I*, *Anabaenopsis circularis* (G. S. West) Miller; *H*, four vegetative threads, the third from the left with two incipient heterocysts; *I*, two threads, the one with an akinete. *J*, *Nostoc coeruleum* Lyngb., small part of a mature colony, with vigorously growing filaments and no heterocysts. *K*–*M*, *Gloeotrichia natans* (Hedw.) Rabenh.; *K*, base of thread with part of a young akinete and a heterocyst showing the ring around the connecting strand; *L*, *M*, threads with terminal heterocysts. *N*, *Stigonema ocellatum* (Dillw.) Thur., part of a plant.

(*Photos*. *R*. *Cullen*.)

A FURTHER CONTRIBUTION TO OUR KNOWLEDGE OF CAULIFLOROUS PLANTS (WITH SPECIAL REFERENCE TO SWARTZIA PINNATA WILLD.).

By J. McLean Thompson, Hartley Laboratories, Liverpool University.

(Plates *6–8*, and a text-figure.)

[Read 5 January 1950.]

Although there have been readings of the cauliflorous state for over seventy years, no proper means of judging them were sought until quite recent times (1, 2, 3). So far, the quest has been for facts of growth and structure and for their bearings on this state itself. In touching now upon the cauliflory of a *Swartzia*, these pages seek to amplify the means.

Initially, it seemed to some, with interest in Natural Selection, that, since the mode of flowering on limbs or boles is far from rare in trees of tropical rain-forests, it may be held a consequence of adaptation; and one attained by gradual steps throughout descent, much as were then the 'special' body-features which some tropical trees display (4, 5). On this approach, it was implied, and later was inferred, that cauliflorous plants have so become, in late descent, through adaptations in their flowering ways to insects fluttering low beneath their crowns (6). It was implicit in this view, and was affirmed in time, that only distal flowering on their leafy twigs had marked the ancestral trees. More recently, these implications have been amplified to meet the facts that bats abound in certain forest regions of the Eastern Tropics and are there constant visitors of many trees which flower on pendent shoots (7).

But while such views have met with some reserve because of many cauliflorous plants to which they could not well apply, their weakness was, and still remains, the lack of evidence from any source that tropical trees which flower exclusively within their crowns are either few or unsuccessful.

It seemed, however, that this state had been essentially explained when Schimper first declared it solely due to dormant buds which had been formed on leafy twigs and which may be in rest for many years on leafless limbs and boles (8). Such buds, he wrote, at last 'break through' the cortices of limbs or boles in which they are embedded and come, forthwith, to open flowering, far beneath the crowns. It seemed to him 'most probable' that, since the bark of many trees in humid forests is of slender growth, or lacking toughness when mature, the obstacles opposed to growth and late emergence of embedded buds are only slight in plants like these and are the only ones to overcome in cauliflorous trees. And since he named the plants observed by him in Java and told how others flower, in various ways, exclusively on thickening shoots or on the boles alone, his view was thought to rest on facts confirmed in some of many plants of which he wrote. Accordingly, he left it to be thought that though *Couroupita* may flower through many years upon its trunk and lower limbs, while some *Anonas* blossom only at the bases of their boles, the flowering modes of all had been essentially explained as due to surface buds. And since his view required no new conception of the ways of plants, there was no cause to think that flowering shoots may be endogenous.

Thus, when the plants now named were first examined in 1922 in the Western Tropics, one was surprised that dormant surface buds could not be found engulfed by bark upon the limbs or boles. And when it proved, instead, that special meristems are organized beneath the bark, wherever flowering is to come, and that these meristems alone give rise to shoots which flower when once exposed, even Schimper's view had ceased to satisfy, and new and special study was required.

Since then, it has increasingly been clear that cauliflory comes in diverse ways the steps of which must first be known to those who seek its causes. Meantime, until a year ago, it had not further been discussed in terms of plant-descent (8).

In this connection, one should notice here that Corner also has inclined to think that distal flowering always marked the ancestors of many trees of modern tropical forests (6). For some, he has proposed that flowers and fruits alike must once have been quite massive things, before a leptocaulous state had yet evolved, and that, for instance, a *Swartzia* may be a cauliflorous tree because its twigs are too precocious for the flowering phases, which are delayed and then fulfilled by dormant buds from which ancestral types of fruit may still be formed on woody stem below. Also, his statements have implied that ramiflory in *Myristica* and other plants is due to kindred causes.

This view cannot, however, satisfy in that *Myristica* may show but local ramiflory ; affecting male and female trees alike. In males, this ramiflory is not due to late inception of the flowering state in dormant buds, but to the late expansion of the leaf-subtended buds which were in flower before their parent twigs matured. The lengthened twigs of female trees may carry fruitful flowers ; even in the axils of their upper leaves, close to the resting tips. When early local branches form on growing twigs of female trees, then often all residual somatic buds remain at rest ; but later flower on ageing leafless nodes. And as to *Swartzia*, it will be shown how bud-successions have their parts to play, and how a local bud-delay in forming spikes, and later flowering through these buds themselves, are factors in its cauliflory. These matters have their counterparts in ramiflory and in cauliflory shown by other plants which flower in cymose ways, and can, perhaps, be best approached by comments now, which may dispense with lengthy explanations in the text. Since flowering shoots in *Swartzia* are not endogenous in any phase of life, it will suffice to call to mind two states with cymose flowering.

It is now known how ramiflory comes in species of *Forsythia*; which form in early summer, once for all, quite short axillary bud-successions upon their lengthened twigs, and how, before the autumn comes, bud-organs have been all defined in strict ascending order (3, 9, 10). These buds are altered much as autumn comes and flowers begin to form, so that the apex of each bud in row becomes a first-born flower. Beneath it, flowers are organized from bract-subtended buds, in strict descending order, so that, in time, the lowest buds may well become the last-formed flowers. This flower-formation often ends while still in early course, so that, ere winter comes, each bud in row may still enclose somatic ones beneath a distal cyme.

Subtending leaves on lengthened shoots may not be fully shed till spring is near, when, at the least, the 'winter' bud and upper ones in each succession are enlarged, in prelude to expansion of their cymes. The lower buds in every row enlarge when spring has come and, in their turn, expand and show their cymes in strict descending order. When buds in each succession number more than four, and also bud-expansion is delayed, the youngest of them all may bloom on thickening nodes.

When forming cymes have not involved their parent buds in full, somatic buds beneath their lowest flowers may die and fall, when summer comes, at thin and corky absciss-layers. More often, when the flowers in cyme above are few, there is a brief delay before they quickly grow, and then form cymes themselves. These lateral cymes derange expansion-order, but have their flowering times before the spring is closed.

Although the ramiflorous species of *Forsythia* have quick-formed bud-successions, they show wide range in fate of buds in row and in the times and speeds of cork-formation. These features bear on when and where the flowering buds expand, as on their spans of dormancy. There is no cause to raise for

plants like these a question of precocious twigs or of delay in flowering-time till buds have come to rest. There is, much rather, question here of buds which are still young when flowering comes, and of delayed expansion. The plants themselves might well be cauliflorous, if parent meristems of buds in rows remained in active budding on the leafless nodes, and new-born buds were brought to flower throughout succeeding years.

It is known, too, how cauliflory comes in *Pleiocarpa*; a shrub which blossoms first in middle life, by simple crown-borne cymes (11). Some features of its earlier life need brief comment since later years bring oft-repeated flowering on its thickened shoots.

Long ere this plant had heightened and composed its crown, each phase of growth had closed with new twigs lengthened and matured, and with each larger leaf, at least, subtending buds in single rows above their parent meristems.

Before each phase had reached its close, the topmost buds in several rows had often given rise to leafy shoots, of which but few had later been retained within the branching framework. In every phase, the buds in row beneath a forming branch had come to rest, once cork had formed upon their parent meristem and brought its time of budding to an end. When leafy shoots did not arise, the time of dormancy had been delayed; and cork had not appeared upon the meristems until the nodes were past-matured. The buds had been somatic as they came to rest, and so had stayed—though some had died—until the plant had ceased to heighten much or flower upon its crown.

Thus, when the time is come at which the twigs extending lengthened shoots are future flowering ones, the last of all somatic buds to form approach their time of rest on nodes matured beneath these twigs themselves; and cork is forming on their meristems which will no longer bud.

In mode of growth and early form, these twigs are like somatic ones, save that their rows of buds are organized before their chief extension comes. When they are lengthened, though still immature, their buds in upper rows, at least, bear distal flowers of cymes whose lowest flowers are formed before the twigs mature. This cyme-formation ends while still in early course, and always leaves somatic buds beneath the lowest flowers. It is complete in every bud before a phase of rest which does not lead to cork-formation on the parent meristems.

When growth resumes, new twigs extend the flowering shoots, and have their rows of cymose buds before they are matured. Also, each first-formed row of flowering buds is lengthened now, by new-born buds which are in cyme ere seasonal growth is closed; without a sign of forming cork on meristems below.

Although the flowering shoots may cease to lengthen soon, each later season brings for them new cymose buds, until the meristems are clothed in cork and budding has been ended. By then, the lower lengths of shoot are seldom less than five years old; yet have but just acquired their youngest buds, with forming cymes within. All branch-borne buds beneath these lengths are still somatic and, mainly, are at rest. The buds on every length have but a season's rest before they broaden and expand in no precise succession. When seed is set, their lower buds are still somatic through a phase of rest, which is prolonged, most often, till the fruits are ripe, and they have been displaced by active growth. Most commonly, the flowers are sterile and are shed as anthers wilt : and then cyme-axes fall ; each at an absciss-layer, the last of which is quite mature before the blossoms fade. Thereafter, lower parts of flowering buds persist as cork-sealed-stumps ; still with the resting buds which cymes had not involved. Like those beneath the fruitful cymes, these buds may be at rest, till flowering shoots have reached their major lengths, and nodes are greatly broadened. At very varied times, now here, now there, they duly grow and quickly come to flower as parent buds had done, and add, in turn

their stumps with buds from which new cymes may form. And since new flowering buds may yearly come beneath the rows of stumps, the ramiflory first displayed may change, in time, to partial cauliflory; though still involving only lengths of shoots which have already flowered.

When distal flowering, now in mind, has mainly run its course, some dormant buds, in rows not far beneath the crown, may alter soon to flowering ones and then expose their cymes. In time, still lower and still lower buds attain the flowering state, till even basal nodes of sturdy shoots may bear their first-born blooms. Throughout this cauliflorous phase, wherever cymes have fallen, stumps remain, with buds which later bear their cymes and lead to further flowering. This latter phase of flowering is prolonged; with growing numbers of the cymes displayed, until the shrub is old.

Herein is long enduring flowering state, from early middle-life; with every cymose bud a starting-point for later ones, and also mounting flowering vigour in enlarging field, so long as ageing lengths of shoot have buds to bring from rest. This vigour comes when crown-borne twigs are rarely formed anew, and, step by step, is then expressed by dormant buds below.

In contrast, when such vigour comes in species of *Forsythia*, it is expressed in part on flowering shoots which grow again in length; but mainly on new lengthy flowering shoots, until the plants are old.

In turning then to state the facts confirmed in *Swartzia*, one thinks a species can but be a cauliflorous tree when, in it, budding-time for leaf-subtended meristems is long; its spikes have basal buds, with growth retard, from which new ones are always formed; and, first and foremost, flowering is not marked, nor does its vigour reach its peak, until the tree has gained its major height; yet still has dormant buds at many levels on its limbs and boles, despite extensive cork-formation. One also thinks that if these buds were lost ere flowering vigour reached ascendency, the limb-borne spikes of any *Swartzia* would be, and could but be, endogenous, as in some species of *Couroupita*, and on the limbs and bole of *Ceratonia* (16.17).

The points of floral structure added to the text may cause at first surprise, but go to show that further study of the Swartzieae is required.

Swartzia pinnata Willd.

One may recall that Aublet first described, and called *Tounatea*, a cauliflorous tree of French Guiana ; that other trees with flowering on their crowns were named *Possira* (1) ; and that, though some were later known as *Rittera*, these and their kindred plants were duly merged in Schreber's genus *Swartzia* (15.5.2).

We owe especially to Willdenow (27, 28) and Vogel (23) early knowledge of some species in Brazil and Venezuela ; including two with clustered racemes on their trunks and ten, at least, which flower upon their crowns.

It later fell to Bentham to supply a basic record of the flowering ways of species in Brazil, and to present a wealth of fact regarding them which still commands our admiration and attention (4). Some mention of the ways which he described are needed here since, to this day, they are well-nigh complete, and mainly need but linkings twixt their two extremes.

For some, he told how racemes are entirely terminal; for others, quite axillary. They may, in some, be all confined to tips of crown-borne shoots ; but, when abundant, then relate to upper leaves as well. In some, they are on lengths of shoot which are but one year old ; in others, on maturer shoots, some distance from the crown. In not a few, they just surmount the current branches' bases ; in others, they are thus disposed to older lateral shoots or may, indeed, be just below the latter's broad insertions. In some, the limbs and

trunk alike are seats of active flowering; in others, during many years, the trunk may be in flower.

He also told of crown-borne racemes, singly or in groups; of rows instead of single racemes often formed at least above or just beneath the lateral branches' bases; of racemes flowering on their distal lengths alone, when borne on slender shoots, and of the fuller flowering often shown on thicker shoots below. He also noted several species in which upper panicles are formed, when racemes bear some fertile basal branches.

We owe to Pittier a clear account of Panamanean and Guatemalan species, known to him as flowering only on their crowns (12). Among them, there is one which Aublet called *Possira*, and one which Bentham had described, and some which Sprenger, Smith and Donn had named, and others of his own quite recent finding.

He noted how some species vary much in stature; as trees, for instance, 6 to 20 m. high, or ranging thus from only 3 to 10 m. in height. He told again of leaf-subtended racemes, singly or in pairs, upon a single plant, and put on record how dimorphic flowers may stand on single racemes. He noted how specific flowering times may be in May or June, or reach from July to September, or have their incidence at least in January, with fruiting late in March. He thus suggested flowering seasons more than once a year, but left untold, as others did, the ages of the species when they first are brought to flower.

From Ducke has come still widening knowledge of the species in Brazil (7, 8, 9). Midst many features which he clarified, one need but note how racemes, branching twice, may often form on sturdy upper leafless shoots of *Swartzia polycarpa*, and simple ones may all but clothe the ageing shoots and sturdy limbs of *S. reticulata* and *S. melanocardia*. He gave the known flowering times for some as July, August, or September, and fruiting times, respectively, in late November or January, and even late in May. It seems he has not told, to date, the age at which a cauliflorous species comes at first to flower, nor where its first-born racemes stand, nor how its flowering course is run.

And lastly, Sandwith has made further plain how species in the forest may be major trees; yet often are quite shrubby plants on river banks or on savannahs (13). He mentioned thus a tree of *Swartzia grandiflora* as 72 feet high, and others, also with the racemes on their limbs, as 40 feet and 20 feet in height. He told of *Swartzia Sprucei* in flower in June, October, and again in March, and of the months of March, July, September, and November as those in which *Swartzia Schomburgkii* is known to flower. He thought, perhaps, the more primitive Swartzias might be large forest trees which flower within their crowns, and that low shrubby habit and the cauliflorous state may be among adaptive changes which have marked descent.

His comments on both simple racemes and panicles which form on younger branches near the crown of *Swartzia oblanceolata* but underline how rarely panicles have been observed; and only then in species, flowering on or close beneath their crown (4, 7, 8, 9). Though Bentham wrote of simple or branched racemes, bearing many flowers, along the trunk of *Swartzia cuspidata* (4), it seems that panicles are still unknown for any species flowering on its sturdy limbs or bole. To some extent, the statement made below may help to make this matter plain.

In giving thus the known though scanty background to the facts disclosed for *Swartzia pinnata*, one would acknowledge here, with special pleasure, how Professor R. E. Holttum gave much valued aid, throughout a year, and noted also flowering times. To date, one cannot tell, with certainty the age at which this species first is brought to flower, or of the early phases of its flowering course. In that it flowers throughout its greater length, from thickening shoots beneath the crown to sturdy lower limbs and upper bole, while yearly

heightening, it well-nigh links the two extremes which Bentham knew, and adds to knowledge of the cauliflorous state.

It may be that the tree considered here was raised from seed in Singapore in 1905; and if this date for sowing is correct, the plant was fifteen years of age when first observed to flower.

Like many evergreens in Eastern Tropics, it proved of slow and intermittent growth. Its height was well-nigh 20 feet by 1948, when—as in previous years—it flowered from thickening shoots beneath its crown to levels low upon its basal limbs; twixt 3 and 4 feet from the ground.

A branching limb is on its short and upright trunk which, followed upwards, seems to end in strong diverging limbs. Three such are low in fig. 1, Pl. *6*, which shows how they, in turn, appear to end where higher ones diverge, and how this forking is maintained by those beneath the crown. The limbs are shown as early in a flowering-phase in April 1949; with burr-like swellings scattered on their lengths; and of most varied size and form. At various levels, curving spikes are clustered on the burrs: for greater part, the naked burrs will later be in flower.

In that this branching-habit closely bears upon the flowering-course, some features of the distal shoots, in rest and growth, are worthy of attention.

When seasonal growth in length is closed for any leafy twig, the latter does not form a distal 'winter' bud; compact or close invested. Instead, its ending is a tiny length of slender hairy shoot; with leaves in seeming pair, and with their pinnae rolled above an obvious apical bud (Pl. *6*, fig. 2). The rachis of the topmost pinnate leaf, matured beneath this shoot, is long and pulvinate of base: and twixt the latter and the distal shoot, as shown now, a sturdy bud protrudes. On sectioning, this bud is proved the topmost one of quite a close and simple row; descending steeply on a gentle curve along the adaxial surface of a narrowing pit, and ending near its floor (Pl. *6*, fig. 3). The tube-like floor is lined by meristem with which the lowest forming buds are merged. As shown now, there are four formed and forming buds in row: the topmost in an early stage of distal leaf-formation. On other twigs, this bud is not advanced in growth, although the largest in its row.

Such rows of buds are at the nodes below, on lengths of shoot which had but been matured. They all may be at rest; and even the topmost ones may still show growth-delay. Their parent lengths of shoot may then be long and straight, although some older lower ones had forked at various nodes.

This forking is foreshadowed once the 'resting' shoot extends to form a current twig. There is then synchronous restricted growth of any upper bud in row within the pit below, although, most commonly, the topmost bud alone is thus involved. Subjacent growth may raise it high and, when continued, makes the current shoot diverge from the older shoot which it extends (Pl. *6*, fig. 4).

Before the current shoot matures, with pinnate leaves expanded, now here, now there on it, a topmost or an upper bud in row may grow apace, and early yield a short but sturdy branch whose lower leaf, together with its row of buds, is quickly atrophied above a short but obvious internode. It may expand a single upper pinnate leaf, before its growth subsides and leaves its tiny 'resting' shoot near to this leaf's pulvinus (Pl. *6*, fig. 5). This 'resting' shoot may quickly be excised by cork, which soon extends on every face, and round the leaf's pulvinus. The cork-formation leaves untouched the leaf-subtended buds; even when the leaf-scar has been sealed, and outwardly displaced. This movement opens wide the axillary pit so that a section shows more freely than elsewhere—and, for the greater part—the buds in row upon the inner wall; and merging with the meristem upon its tiny floor (Pl. *7*, fig. 6). The growth beneath such branches soon subsides; thus leaving current shoots

above still undisplaced, and with proved prospect of a later growth. Quite frequently, these branches are excised, with all the buds with which they are in row, once cork has formed athwart their bases and beyond. Thus, forking which they early promise is unrealized : and, neath their broadening scars, no later flowering comes.

This forking is, however, realized when any forming branch upon a current twig co-equals it in growth, or, springing from a topmost bud, soon gains a marked ascendency. Equality is often near or reached when branches form from upper-middle or mid-upper buds ; while topmost and the lowest ones in row remain quiescent at their bases. In fig. 7, Pl. 7, is seen, in greater part, a current twig in early growth, diverging to the left : to right, a branch, diverting it, ascends in line with older shoot below. An upper-middle bud had formed the branch : the topmost bud in row protrudes above its base. Above the leaf-scar neath this base, a lower bud is seen. Whereas the pinnate leaves are long retained on lengths of shoot matured from twigs whose growth was in ascendancy, they are shed early at the forks, with current twigs displaced.

Thus, as ascendant and diverging shoots are full-matured within the crown, they yet have buds in rows, at nodes where branches stand ; in part above, or all below the points of branch-insertion. These buds are small, and scarce protrude at older thickening nodes ; even where the branches may be short and forking is not shown (Pl. 7, fig. 8).

The shoots have also middle-rows of buds, topped by late-forming branches whose closest neighbours have the rounded head which marks all buds ' at rest ' (Pl. 7, fig. 9). The branchless basal nodes have rows of buds which number six or seven : much later seen as mammillae above the ridged leaf-scars (Pl. 7, fig. 10).

In noting then that, in this plant, all new-formed shoots arise on only recent twigs and branches in its canopy, and that their seasonal forming-time is short, one thinks the mode of body-growth has been unchanged from youth, since branched and strongly forking limbs, as shown in fig. 1, Pl. 6, but magnify the minor crown-borne shoots, formed with each seasonal growth. And since its distal lengths of shoot are all alike in mode of bud—and branch-formation, one may then turn first to trace the fate of ' resting ' buds they bear, and of the meristems below.

As shown in fig. 9, Pl. 7, when twigs mature, the upper ' resting ' bud in any row is short of axis and untapering. Unlike a forming branch, it has a broadly rounded head. As younger buds beneath it indicate, its leaves show growth-advance. These leaves mature, in time, as short and pointed scales which each subtends a compact row of buds ; but shorter than is any one upon the parent shoot (Pl. 7, figs. 13 and 9). As proves, its axis-tip alone provides a current flowering spike ; and this not till the bud itself is over two years old.

Once new twigs have extended lengths of shoot, the latter's rows of buds show little outward change until their parent nodes are nearly two years old ; save that the topmost buds are full-exposed, while others slowly swell. Before subtending pinnate leaves are shed, the rows are raised to various heights on internodes above respective broadened nodes ; and all protruded buds are then displaced, though still arranged in curve. These latter buds most often number more than those at higher nodes some distance from the crown. This also holds for lower buds, still hidden in the pits : and, always, lowest buds still merge with meristem upon the floors. There is then little cause to doubt that, through the ' resting ' phase for buds which early formed, from time to time, the meristems resume their bud-formation.

Once upper buds have been displaced, there is no single sectional plane in which they all are shown: much less one passing through a row complete, down to its pit's small floor. Thus, while but three protruded buds are seen in fig. 11, Pl. 7, there stood in other planes, two larger higher ones, and one

much smaller than the lowest shown. For greater part, this smaller bud was still within the pit : its rounded head but just surpassed the latter's narrow mouth. The figure shows the pit and tiny buds in only upper length; inclining inwards, on descending course, beneath the buds exposed. This figure is to less than half the scale employed in fig. 9, Pl. 7. Its lower part is internode on which the buds were raised. Between them and the curving leaf-scar at its base, thin cork had just been formed. This cork-formation marks the end of internodal growth in length. It soon invests the bases of protruded buds, and later reaches to the pits' short lower rims. Thereafter, often only upper 'resting' buds extend their tips to form quite slender curving spikes (Pl. 7, fig. 12). In this, the lower axis of each bud involved remains extremely short, so that its scales, with rows of buds, are soon engulfed in cork. The upper internodes may lengthen much, so that as pictured here, their scales are raised and full-exposed beneath the lowest flower. Whereas they also have subtended buds in short and simple row (Pl. 7, fig. 13), each flower-subtending scale above has but a single bud. Extended internodes between the flowers may vary much in length ; and here and there, flower-buds are shed and leave their cork-sealed scars.

As to the levels neath the twigs at which these spikes extend, Professor Holttum gave them, late in May of 1949, as ' no nearer than about 2 ft. from the end of a branch. This distance is in many cases 3 or 4 ft. ; or even more on spreading lower branches '. He noted also that their parent nodes are three years old, or more, and that his measurements were made when major branches, reaching to the crown, had many burrs along their lengths ; with spikes in open flowering. In that this flowering phase began in early April, and was well-nigh at climax when he wrote, it seems the shortest resting-time for upper buds in rows is fairly surely known.

Unlike protruded buds beneath a raceme's base, these still in pit remain in row ; though sometimes placed obliquely to their broadening node. They, and protruded ones alike, may all be still 'at rest' ; even when the raceme falls and leaves its stump with buds : and later, some protruded buds may form extending spikes ; though they are, doubtless, five years old, or more. There have been seen some four-year nodes, with racemes forming from the buds in row beneath quite recent stumps. The pits with shrunken buds below were much deformed, and lined by cork; as commonly, at older nodes. It thus appears this species, too, may carry clustered racemes.

The stumps of fruitless racemes are quite narrow, while those of fertile ones are broad, and often raised (Pl. 8, fig. 14). The number of the buds retained on them is never high; but varies with the levels of the absciss-layers.

The short remaining span of life for buds in rows, still resting in the pits, must also vary, node by node; since shrunken rows, neath racemes' stumps, were proved on four- and five-year nodes ; while quite undamaged ones were found on nodes, a little older. The fragments of such rows are found beneath the minor upper burrs. Even prior pit-positions have remained in doubt beneath the larger burrs observed, once crumpled and, it seems, continuous cork has clothed their lower margins.

To date, new bud-formation from a pit's small floor is proved no lower than some flowerless nodes which might, at most, be six years old.

But since it is not often far below the six- and seven-year nodes that racemes spring anew, from buds on recent stumps, and from such buds alone, the starting-points of burrs are fixed, once racemes formed from them have left their stumps with buds ; enlarging on the old (Pl. 8, fig. 15).

It is, then, close beneath the nodes where first-formed racemes fell when flowering phase had passed, that new ones spring from buds on forming burrs, in an ensuing phase ; through which, also, still further racemes form on larger burrs ; spaced on the limbs below. And since each growing season brings new

distal rows of buds in some of which new racemes duly form, the flowering from the buds in rows above and that from burrs below proceed, in time, together and without a gap between ; and is repeated thus, once each new growing season has been closed.

As to the burrs at scattered points along the sturdy limbs, they vary in fertility, as in both size and form. In contrast, major ones are those which have already many budding-stumps ; most often raised and broad : these burrs are sometimes forked (Pl. *8*, fig. 16). Whereas a larger burr is shown now, as in a flowerless phase, when flowering season comes again, it and its likes soon carry spikes anew ; yet may retain maturing fruitful ones which sprang from broadened stumps (Pl. *8*, fig. 17).

The larger burrs, now here, now there, may give no outward sign of flowering state throughout a lengthy season, while others carry racemes, in very varied numbers. The bark of parent limbs is deeply rift, and falls in sheets, while burrs extend their spikes. Yet burrs do not discard their cork nor ever are excised ; though close-investing cork is lost around their broadened bases (Pl. *8*, fig. 18). The burrs on lower limbs, from 3 to 4 feet from the ground, have proved to flower again.

The little known of flowering-times is told in Holttum's letters. Some extracts, with the letter-dates, can well depict the way in which a flowering-phase proceeds.

31. 12. 1948. ' The tree has now some young fruits, but no flowers '.

17. *3. 1949.* ' The tree has now completed a new growth of leafy shoots, which are still green '.

24. 3. 1949. ' At present, a few (burrs) are flowering, and a few very young inflorescences are starting to elongate '.

19. 4. 1949 and *13. 5. 1949.* In letters of these dates, progressive flowering was recorded.

31. 5. 1949. ' There is now a big flowering ; and the main branches, right up into the crown of the tree, bear many inflorescences '.

21. 6. 1949. ' The inflorescences have now dropped all their flowers '.

11. 7. 1949. ' The tree has only a few inflorescences forming now ; but it seems that more are coming '.

29. 7. 1949. ' A very big flowering is beginning. A large portion of the old inflorescence-burrs have new inflorescences ; and I have gathered what seem to be the earliest stages of inflorescences developing on small branches ; i.e. inflorescences appearing where no burr existed already '.

If one considers features here described, it will appear that, as this tree is now, the flowering of its crown-borne buds in rows is long delayed ; and that the ramiflorous state is reached when some expand as racemes. Throughout, its crown acquires new leafy twigs, with rows of buds which suffer like delay.

The first-formed racemes only flower along their upper lengths ; and when they fall, their stumps remain, with buds for later flowering.

Likewise, each later raceme leaves its stump, with buds, upon the parent one : so that, as stumps are added, burrs are formed, and further come to flower.

Thus, as the crown is ever raised above the ageing nodes, the limbs are brought, by gradual steps, to cauliflorous state ; while ramiflory is maintained on branches neath the crown.

Since nothing more than budding-stumps, which flower again, compose the limb-borne burrs, it seems the flowering-mode has been unchanged from early years : the sapling, with its ramiflory : in time, the heightening tree, with added cauliflory.

If one considers, too, the points discussed in *Pleiocarpa* and *Forsythia*, it will appear their flowering-modes throw light on that of *Swartzia* : and this apart from inflorescence-form ; the former cymose, and the latter racemose.

As flowering is increased, through many years, in *Pleiocarpa*, and largely finds expression through the stumps of cymose buds, also this tree flowers more and more through those of former racemes.

A Note on Floral Structure.

Some points of floral structure merit note since none, it seems, have been recorded ; and floral plans have left in doubt where stamens and carpidia are formed (10). The features mentioned must, of course, be later judged by those of other species (Pl. *8*, fig. 19).

The forming flower is first a small and bract-subtended dome ; and sepals spring upon its margin.

The dome is then deformed, as sepals merge upon a rising torus, which leaves the dome deformed within a narrow moat ; soon filled with new primordia.

From one of these, a petal forms. Its opposite, within the moat, supplies the one carpidium. The latter's neighbours, right and left, give rise to major stamens ; while all remaining in the moat mature as minor ones. The major stamens' counterparts are carpidia in several other species.

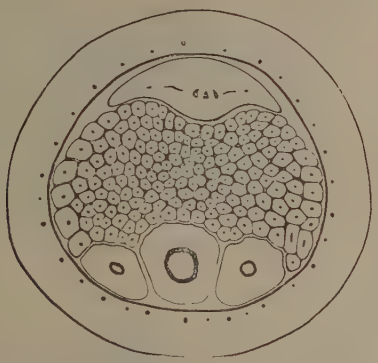

FIG. 20.—Diagram illustrating the floral structure of *Swartzia*.

The dome itself gains little height, but is much broadened on the side where major stamens and carpidium will stand. On mounting from the carpidial base within the moat, its summit may be reached along a long and gentle slope, or by a short and steep ascent, beginning at the petal-base.

Once organs in the moat are all defined, new ones arise upon the dome, in close ascending sequence, until they clothe its surface. These organs all mature as minor stamens ; much of a length with those within the moat.

To some extent, these points may be conveyed by fig. 20 in the text. The calyx-tube is shown as undivided rim : the petal-base, as with a foliar form. Opposed to it, the carpidial base is twixt the filaments of major stamens. All minor stamens from the moat and dome are represented likewise. These minor stamens number 173. They may be formed in greater or in smaller numbers. They form a single group in fig. 19, Pl. *8* ; neath the petal, and ascending from the point at which the long twin-stamens and the curving pod pass to the moat which sepals fringe.

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DESCRIPTION OF PLATES *6–8.*

The description of the Plates is given in the text of the paper.

LECTURES AND DEMONSTRATIONS ON THE PRACTICE OF BOTANICAL AND ZOOLOGICAL CLASSIFICATION

In conjunction with the Systematics Association, the following Lectures and Demonstrations were given to advanced University Students during the Session 1949–50. The Lectures were given in the Society's Meeting Room, with the exception of the Demonstrations as stated below.

' Dealing with the Raw Material (Plants) ', by Mr. B. L. Burtt, F.L.S.

' Dealing with the Raw Material (Animals) ', by Prof. Alastair Graham.

' Fossils in Classification ', by Dr. A Tindell Hopwood, Sec.L.S.

' Geographical Distribution and Classification (Plants)', by Mr. A. J. Wilmott, F.L.S.

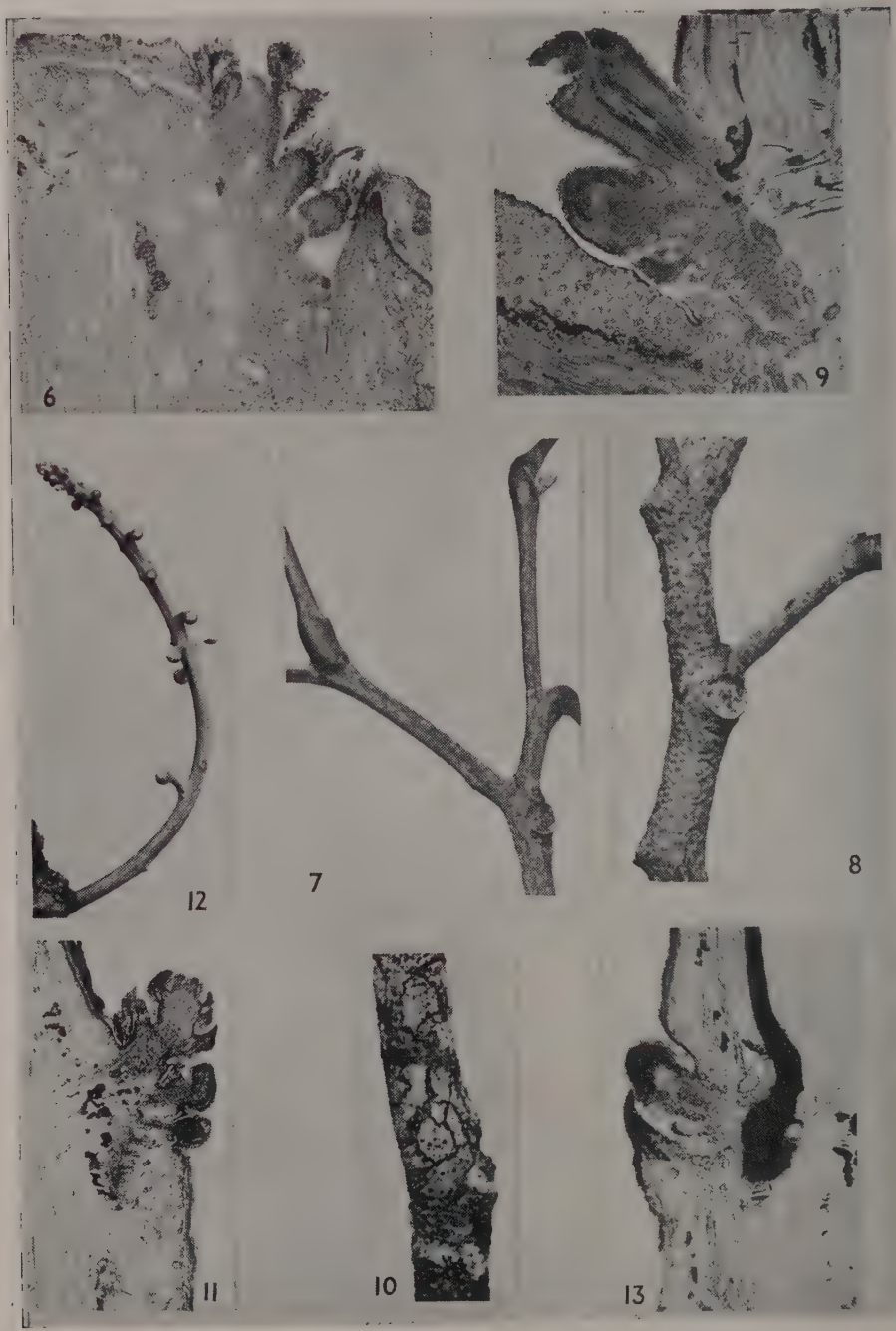
' Geographical Distribution and Classification (Animals) ', by Prof. G. D. Hale Carpenter, M.B.E., F.L.S.

' Cytology as a Factor in Classification ', by Colonel F. C. Stern, O.B.E., M.C., F.L.S.

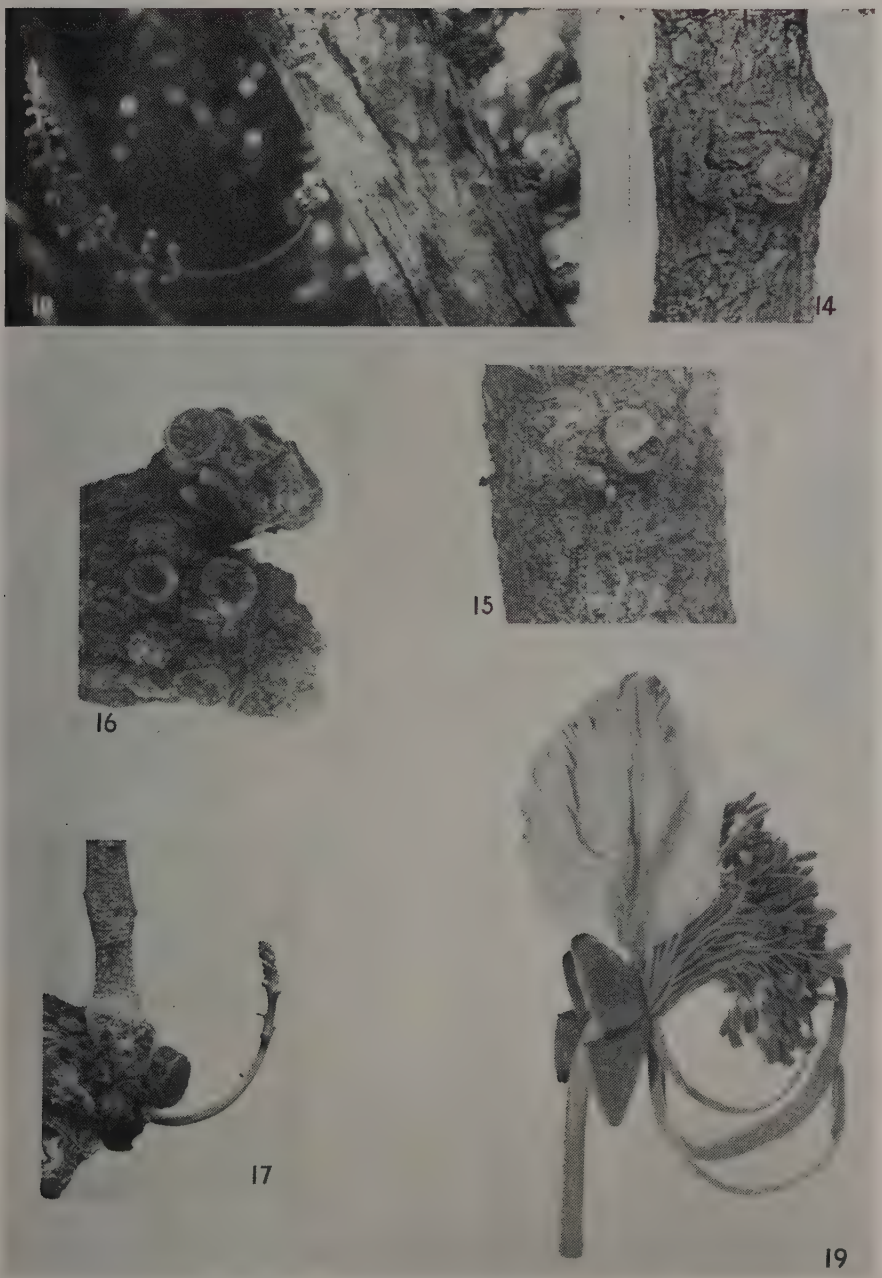
Demonstration.—Held at the British Museum (Nat. Hist.), Cromwell Road, S.W.7, at 3.0 p.m., by kind permission of the Trustees.

Demonstration.—Held at the Herbarium, Royal Botanic Gardens, Kew, at 2.30 p.m., by kind permission of the Director.

Swartzia pinnata Willd.



Swartzia pinnata Willd.



Swartzia pinnata Willd.

OBITUARIES

On 28 April 1950, Professor **Oakes Ames** (1874–1950) passed away at his winter home in Ormond, Florida, in his seventy-sixth year. Internationally known, particularly as a leading orchidologist, his botanical and horticultural activities were devoted with equal success and enthusiasm to research, to teaching, and to administration for more than half a century at Harvard University.

Son of Oliver Ames, a financier and once Governor of the Commonwealth of Massachusetts, and Hannah Coffin Ray Ames, and grandson of Oakes Ames, one of the builders of the Union Pacific Railroad, Oakes Ames was born in North Easton (near Boston), Massachusetts, on 26 September 1874.

His interest in horticulture and botany began early in life, ' when, as a boy, he joined his father . . . in the hobby of collecting and identifying the wild flowers of the New England countryside. Young Ames, setting for himself the goal of learning the name of one new plant each day, began a serious study of the local flora of North Easton, and, with a tin biscuit box to serve as a vasculum, he roamed the woods and countryside, imagining himself to be exploring strange and distant lands '*.

He prepared for his university career at Noble and Greenough School in Boston and entered Harvard College in 1894, receiving his A.B. in 1898 and his A.M. from the same institution the following year.

Immediately after receiving his A.M. degree, he began his teaching activities at Harvard, serving from 1900 to 1910 as Instructor of Botany. In 1915, he was named Assistant Professor of Botany, a chair which he held until 1926 when, under President A. Lawrence Lowell, he was appointed Professor of Botany. He served his University in this capacity for six years. Then, from 1932 to 1935, he held the chair of Arnold Professor of Botany and, from 1935 to 1941, Research Professor of Botany. In 1941, Ames retired from his teaching duties, holding the title of Research Professor of Botany, Emeritus, until his death. In 1927, he was named by President Lowell as a member of the Administrative Board of the Graduate School of Arts and Sciences, and, in 1929, as Chairman of the Committee on General Examinations.

Although it is difficult, if not impossible, to consider Ames's teaching and research apart from his administrative activities, so closely were they allied, we may enumerate his administrative appointments separately. From 1898 to 1909, he served as Assistant Director of the Botanical Garden, taking over its complete administration as Director for the next thirteen years, from 1909 to 1922.

As early as 1900, Ames, with Professor George Lincoln Goodale, was influential in persuading Mr. Edwin F. Atkins of Boston to establish the Atkins Garden in Cuba. Ames administered this as a dependency of the Botanical Garden in Cambridge for a number of years, since President Lowell refused for some time to grant the Cuban Garden independent status as a branch of the University. Ames's efforts on behalf of the new-born tropical garden, though not officially recognized by the University, are recorded in his annual reports to the President.

In 1923, he became Curator of the Botanical Museum, a post he held until 1927, when he was appointed Supervisor of the same institution. Later he was named Director of the Botanical Museum by President James B. Conant. He filled this post with characteristic enthusiasm from 1937 to 1945, when, at his own request, he became Associate Director, relinquishing active administration but preserving, until the time of his death, a vital interest in the current research and publications of the Museum.

* All the quotations marked with an asterisk in this notice are from the biographical sketch by P. C. Mangelsdorf in *Orchid in retrospect*, by Oakes Ames (1948), ix–xv.

One of the most demanding of administrative periods during Ames's half century of service at Harvard was from 1927 to 1935, when he was Chairman of the Council of Botanical Collections and Supervisor of the Biological Laboratories as well as of Harvard's Botanical Garden in Cuba and the Arnold Arboretum. This exacting appointment followed the brilliant work he carried out as Chairman of the Committee on the Future Work and Needs of the University in Biology, a post to which he was named in November 1926 by President Lowell.

During this whole period, Ames was active in enlisting additional financial support and in creating new entities for biology at Harvard. As Supervisor of the Arnold Arboretum, he more than doubled the endowment of that institution by raising the Charles Sprague Sargent Memorial Fund. The Biological Laboratories at Harvard owe much to his efforts and foresight, for, as Chairman of the Building Committee and subsequently as Supervisor of the Biological Laboratories, he was a leader in drawing up the plans and constructing the large and modern building now housing most of Harvard's experimental biology. Furthermore, he was instrumental in raising extensive financial support for this building and, later, he guided the difficult pioneer amalgamation of three independent departments into the single Department of Biology.

It has truly been said of Ames : ' Seldom in the history of Harvard University has one man been called upon to fill so many important posts '*.

When Ames was still a very young man, he became deeply interested in the orchids. It was apparently through two steps that Ames entered into orchidology. One day, as a boy, he went into his father's room and noticed two flowers of *Dendrobium nobile* in a glass on a table at his father's bedside. These two lone flowers shed such a warm diffusion of colour on the otherwise dull scene that Ames was magnetized by their beauty. The second step—and the one which crystallized his resolution to devote his academic life to the orchids—was a conversation with Doctor N. L. Britton of the New York Botanical Garden. Sensing the young man's keen interest in the orchids and appreciating in him qualities of a sound taxonomist, Britton pointed out to Ames that the classification of the Orchidaceae was almost hopelessly confused and infantile. He put it to Ames that to make order of this chaos would need not only a brilliant taxonomist but extensive financial support. Finally, he suggested that since Ames had the interest, the ability and the wealth, he make the orchids his field. Ames took the suggestion and immediately began to amass material on a large scale. This decision ' has borne rich botanical fruit ' for ' to-day, and in no small measure because of his work and that of his associates, the species of the Orchidaceae have probably been more thoroughly studied and more completely classified than those of any of the other larger plant families '*.

The large collection of living orchids which he had built up at his home at North Easton, where he also established the Ames Botanical Laboratory, led him deeper and deeper into an inquisitiveness about the classification, structure, and function of the orchids. Eventually, he donated this living collection to the New York Botanical Gardens, and gradually transferred most of the Ames Botanical Laboratory to the Harvard Botanical Museum in Cambridge, concentrating his major research efforts in the field of orchid taxonomy.

The Ames Orchid Herbarium, which now comprises 65,000 critically determined specimens as well as large numbers of line drawings, tracings, and photographs of type material from the large orchid herbaria of Europe, has become the largest single orchid herbarium in the world. No expense was spared in the building up of the collection, and Professor Ames went so far as to finance in part several expeditions to unexplored regions of the world in an attempt to perfect the representation of orchid material in his herbarium. Only the Lindley Herbarium at Kew and the Reichenbach Herbarium in Vienna

are comparable in scope; and the Ames Orchid Herbarium has become the centre for most of the taxomonic studies on the orchid flora of the Philippine area and of the New World. His herbarium is unique in having an extensive collection of critically determined floral dissections preserved on glass slides in small tin cabinets, an invaluable aid in rapid determination of new material and in monographic work. Professor Ames gathered together an unusually complete working library of orchid literature, including current journals, from all parts of the world; it forms an integral part of the herbarium. Both the herbarium and the library, now housed in the Botanical Museum in Cambridge, were given to Harvard University by Professor Ames in 1941.

In 1904 and 1905, Ames began to publish important taxonomic contributions in the orchid family and, in 1908, he agreed to write up the Orchidaceae for the 7th edition of *Gray's New Manual of Botany*. His interest and activity in this family soon widened, however, when, in the same period, he undertook the vast task of identifying the orchids of the Philippines, becoming eventually the leading authority on the family in that part of the world and describing hundreds of species new to science. It was early apparent to Ames that nothing could be accomplished without access to the type or classical collections which his European predecessors, Lindley, Reichenbach, and others, had accumulated and studied. Accordingly, in 1905, he left for a tour of study of important European orchid collections and, with his two assistants, Mr. R. G. Leavitt and Mr. A. A. Eaton, he visited Kew and the British Museum, the Musée d'Histoire Naturelle in Paris, and the Rijksherbarium in Leiden.

Ames's work on the orchids became even more extensive and gradually embraced many other parts of the world, especially Florida and the Caribbean area as well as Middle and South America. The collections of Ames and Eaton in Florida led to the publication early in his career of an article entitled *Additions to the Orchid Flora of Southern Florida*. This interest in the orchids of Florida, where Ames spent every winter, continued all through his life and was the basis of a number of papers and, very recently, of an extensive book. This book, entitled *Drawings of Florida Orchids*, he published jointly with Mrs. Ames who had done all of the illustrations throughout his years of research. His studies of the orchids of Middle and South America prompted him to make trips to Honduras and Brazil. In a little brochure entitled *Rediscovery of a Lost Orchid* he tells the story of his almost accidental finding of an orchid which had never been seen since the type collection.

Professor Ames was fortunate in having as his life-long companion Blanche Ames, an accomplished artist who illustrated all of his technical papers with extraordinarily artistic and accurate line drawings and etchings of the hundreds of new species. This close collaboration between Professor Ames and his wife is almost unique in the history of botany and has led to the publication of some of the most delightful works ever to appear.

In 1922, as soon as the Reichenbach Herbarium was opened after it had, in accordance with Reichenbach's will, been sealed from botanical eyes for twenty-five years, Ames and his wife visited Vienna for an exhaustive study of types in this collection. Mrs. Ames executed drawings and analytical sketches of most of the essential material in the Reichenbach and other herbaria for the Ames Orchid Herbarium. Of these two co-workers it has been said: 'Seldom in botanical history have science and art been so happily and fruitfully joined'*.

For eighteen years, from 1905 to 1922, Ames, with his wife and sometimes with his collaborators, published a series of seven fascicles entitled *Orchidaceae: Illustrations and Studies of the Family Orchidaceae*. Included in these fascicles was a diversity of taxonomic studies comprising the descriptions of new species from the Philippines, British North Borneo, and tropical America, monographic work of North American genera such as *Habenaria*, *Pogonia*, and *Spiranthes*, and miscellaneous nomenclatural transfers. This series of fascicles gave way,

when research began greatly to increase the output of orchid studies, to a series of papers called *Schedulae Orchidianae* which, with the collaboration of Charles Schweinfurth, appeared in ten numbers, extending from 1922 to 1930. Ames, Hubbard, and Schweinfurth's *The Genus Epidendrum in North and Middle America*, published in 1938, will long remain a model of painstakingly exact taxonomic work.

In recent years Professor Ames's writings on the orchids, which have tended to be more philosophic than descriptive, have shown an astonishingly wide range of interest and a profound understanding of all aspects of orchidology especially the lore of orchidology in the medieval herbals. These papers cover a diversity of topics. He frequently contributed articles to the American Orchid Society Bulletin and wrote the *Enumeration of the Orchids of the United States and Canada* for the American Orchid Society.

Ames's bibliography, published in the Journ. Arnold Arboretum, *31*, No. 4, 1950, numbers more than 300 papers or books on orchids, and in these he described more than 1000 species new to science.

Although Oakes Ames will undoubtedly be remembered primarily as the leading orchidologist of his day, he devoted much of his time and interest to economic botany and has so profoundly influenced thought and teaching in this broad field that he must be counted one of the outstanding economic botanists of this century. Accepting the broad definition of this discipline as a study of plants useful or harmful to man in their relation to human progress, he built up at Harvard something unique in biological research and teaching.

Ames's first contact with economic botany came during his association with Professor Goodale, his predecessor at the Botanical Museum, who had begun to assemble material and data for exhibits and teaching in economic botany. In 1909, Ames himself taught a course which he entitled 'Outlines of Economic Botany'. His serious interest in the subject took deep roots in 1914 and 1915 when Professor East invited him to offer a course in botany at the Bussey Institution of Applied Botany at Harvard.

As a graduate student, Ames was unable to understand the prejudice on the part of some of the leading taxonomists of the day against including cultivated or useful plants in the herbarium and their scorn of applied science. He began to accumulate his own herbarium of plants, wild and cultivated, upon which civilized and primitive man depends for his life. This herbarium, now housed in the Botanical Museum and known as the Economic Herbarium of Oakes Ames, has grown to include 18,000 specimens; it was given to the University in 1940. At the same time, Ames continued to increase the general collection started by Goodale, until, to-day, it is an enormous and enviable collection of plant parts, fibres, woods, extracts, and other products which are basic to teaching and research in the field.

Together with the herbarium and products collection, Ames accumulated a unique library of literature on useful plants. This library, now known as the Oakes Ames Library of Economic Botany, he loved to refer to as a 'gentleman's library'; it comprises approximately 16,000 volumes, pamphlets, theses, and reports and has, in addition, a newspaper clipping file. The library covers all aspects—botanical, anthropological, geographical, pharmacological, chemical, and agricultural—of useful plants, exclusive of ornamentals. It is most completely indexed as to author, subject (by vernacular and technical name), subject heading, and plates: the work of Ames himself and his associate, Mr. F. Tracy Hubbard. The economic herbarium and library were assembled at great expense of money, time and research, and together form a unit unexcelled for completeness in the world. With this extensive and unique background available to his students, Ames offered his course in economic botany, a course carried on and enlarged to-day by his successor, Professor Paul C. Mangelsdorf. This course, one of the most outstanding in Harvard College, has long been noted for its breadth of outlook and its interdisciplinary character. It was, in fact

only in economic botany that Ames taught, since no formal courses in the University were ever offered in orchidology. Besides this yearly course—taken eagerly by concentrators in biology, in pre-medical studies, and even in the classics—Ames gave a course in economic botany and carried out research in poison plants at the Harvard Medical School. Although Professor Ames might not have admitted it, he thoroughly enjoyed teaching. Using completely unorthodox methods (preferring to call his lectures 'chats') and utterly disregarding fact-cramming, he succeeded in quietly guiding his students into paths of original research which often led them to fields far removed from his own.

Ames's publications in the field of economic botany are few but outstanding. His book *Economic Annuals and Human Culture*, written in 1940, has taken its place as one of the most outstandingly original contributions to the whole philosophy of the inter-relationship between plants and man. Written in his clear and concise style, this book advances a number of novel ideas which have already begun deeply to affect anthropological and ethnobotanical thought. He set forth and developed the thesis that all civilization was dependent upon the angiosperm seed which gave man the chance to invent agriculture; that, later, the seed provided leisure time for him to develop arts and crafts; furthermore, that the annual habit of growth had made it possible for man to subdue plants to his will and to create great surpluses which increased the amount of leisure time available to him. He argued strongly and convincingly, on the basis of the evidence of the extreme advancement and specialization of our cultivated food annuals, for a far greater age for agriculture, especially in the Americas, than anthropologists were prone to allow. Ames lived to see the soundness of his thesis gain support by several extraordinary archaeological finds which have recently been made.

One of the greatest contributions to the teaching of economic botany, but one which, unfortunately, has never been published, is the so-called 'Ames Charts' upon which his course in economic botany at Harvard was based. These are charts showing in the form of a tree the phylogenetic relationships of the more important useful plants. Planned out by Professor Ames and beautifully executed in water-colour by Mrs. Ames, they have served to orient many a young man overwhelmed with the complexity of plant classification systems.

During World War I, Ames was drafted to serve on the Botanical Raw Products Committee of the National Research Council. One of the results of his activities for this Committee was the assembling of a large index of economic plants which to-day forms one of the bases of the Oakes Ames Library of Economic Botany. This index has served its purpose in helping to train economic botanists, and Professor Ames lived to see a number of the men he trained serve the United States Government during World War II as botanical consultants and technicians in the search for rubber, quinine, and other products essential to the war effort.

Although far afield from his own personal interests, palaeobotany also felt Ames's influence. It was largely through his own efforts that Mr. William C. Darrah came to Harvard and began research and teaching in palaeobotany.

An artist and perfectionist at heart, Professor Ames insisted almost fanatically upon the highest quality in paper, printing, and composition to set the highest of standards in scientific publications. He deplored the increasing cheapening of paper and printing in our modern scientific journals. Most of the earlier orchid work of Ames and his associates was privately printed by the best presses in New England. When he became Director of the Botanical Museum, however, Professor Ames decided that an institution as active in such diverse botanical endeavours as he planned to make the Museum needed its own journal. Accordingly, he founded the 'Botanical Museum Leaflets of Harvard University'. This review, issued irregularly in ten numbers to a volume, handsomely illustrated and printed artistically by hand-set type on high-grade paper, is now in its

fourteenth volume and is an outlet for research done by members of the Museum staff. He patterned it to cover a wide range of topics, including orchidology, economic botany, ethnobotany, genetical studies in economic plants, history of cultivated plants, general taxonomy, and palaeobotany. The Leaflets, as well as occasional books by members of the Museum staff, are published at the Museum on a press which Ames installed for this purpose.

In 1924, the Gold Medal of the American Orchid Society was awarded to Professor Ames for eminent service to orchidology, and five years later he was the recipient of the Centennial Medal of the Massachusetts Horticultural Society for his researches in orchidology. He earned the George Robert White Medal of Honour in 1935 for eminent services in horticulture. In 1938, he was awarded the honorary degree of Doctor of Science by Washington University.

Oakes Ames esteemed very highly his election on 7 December 1905, as Fellow of the Linnean Society of London. He was a member and vice-president (1923–1926) of the New England Botanical Club, an honorary member of the American Orchid Society and one of its vice-presidents from its inception in 1921 until his death, honorary vice-president of the Canal Zone Orchid Society, a member of the American Academy of Arts and Sciences and Sigma Xi, and Fellow of the American Association for the Advancement of Science. He belonged to many other learned societies.

Such a full scientific life did not create a one-sided man of Oakes Ames, for his extra-academic activities were diverse and demanding. During his university years, from 1895 to 1898, he served in the Light Artillery of the Massachusetts Volunteer Militia. He was long active as administrator of several large endowments and estates and was associated with a number of financial and business establishments. At school, he played baseball, and all during his life he followed professional baseball enthusiastically. A lover of fine music and literature, Ames amassed at his home a superb library and he spent much of his time in the study of the classics, Elizabethan English literature, and some modern writers of whom he particularly enjoyed Conrad and Tomlinson.

On 15 May 1900, Professor Ames married Blanche Ames of Lowell, Massachusetts, and six years later established their life-long home—' Borderland '—at North Easton. He is survived by Mrs. Ames and by four children.

Ames belonged to one of the oldest of those New England families to which the country owes so much. Born into a background of culture and wealth and deeply conscious of his family connexions, he seemed to feel that he was but a trustee of his rich heritage. Be that as it may, he turned the benefits of his heritage to the service of his fellow man through his chosen field of botanical endeavour. One of his colleagues has expressed this facet of Ames's life by saying : ' He never asked but was always giving .'

Ames has rightly been called a ' perfectionist '. His search for the best in all of his scientific endeavours is well known in botanical circles where the factual accuracy of his writings and the completeness of his plant descriptions is so well appreciated. His more philosophical writings sparkle with musical preciseness, and the most abstruse topics are treated with a delightful sprightliness which is often crowned with his whimsical humour. The constant striving towards perfection which early led him to choose the writings of Spenser as his model is seen in his most learned volumes and in his most casual letter.

Like so many other New Englanders, Ames was conservative in politics and liberal in religion. He found little or no conflict between his scientific and his religious philosophy ; perhaps the two were one to him. He frequently told his students that they ought to approach their scientific careers with the humbleness which Tennyson expressed in his ' Flower in the crannied wall ' ; advice not often heard in these days of materialism.

Richard Evans Schultes.

Frederick James Chittenden, O.B.E., F.L.S., V.M.H. (1873–1950), the son of William Chittenden, was born at West Ham on 25 October 1873. He was educated at Leyton, at Carpenter's Institute, Stratford, and at the County Technical Laboratories, Chelmsford, now the East Anglian Institute of Agriculture; it was here that, in 1900, he became a staff-lecturer, having begun teaching in 1889 and subsequently lectured on botany at the Woolwich Polytechnic.

When, in 1907, the activities of the Royal Horticultural Society at Wisley were extended and a laboratory was built, Mr. Chittenden was appointed the first Director; and thus began the long association with the Society that was to continue for the rest of his life. In 1931 he was appointed to the wider post of Director of the Gardens, and during this period, from 1908 onwards, he combined with his other duties the Editorship of the *R. H. S. Journal*. In addition, all the important educational work undertaken by the Society came under his supervision, in fact his influence on horticultural education for many years was much greater than is sometimes realized. The papers for the Society's examinations were usually set by him, or at least the final drafting came before him for approval, so that he has very markedly influenced the Society's educational policy.

By 1931 the work of the Royal Horticultural Society had increased enormously, both at Wisley and at Vincent Square; re-arrangements were therefore necessary and it was decided that the Journal, with other publications, should be edited in London. Mr. Chittenden then accepted the posts of Editor of the R. H. S. Publications, Technical Adviser and Keeper of the Library, the Gardens at Wisley being placed in the capable hands of Mr. R. L. Harrow. Apart from the *Journal* and various annual publications and pamphlets, Mr. Chittenden prepared the excellent *Index to the R. H. S. Journal* for the years 1838–1935, a work of such precision that it serves as a reference book for any matter that the *Journal* has ever touched on; during the war he prepared the ten-year Supplement, which brings the *Index* up to 1945. Descriptions of the plants which received the Award of Garden Merit were published in the *Journal*, and later under the title *Some Good Garden Plants*, the first two editions being the work of Mr. Chittenden. He contributed a number of papers on horticultural and scientific subjects to the Society's Journal and others, and also wrote *The Garden Doctor*, a helpful little book for the gardener on pests and diseases.

In 1939 Mr. Chittenden relinquished the Editorship of the Journal and other posts he then held to undertake the arduous task of revising and amplifying Nicholson's *Dictionary of Gardening*, to be published as the *R. H. S. Dictionary of Gardening*; this work would in any case have taken several years to accomplish and the war was responsible for some delay, but it is much to be regretted that, though well advanced in preparation, it had not been completed at the time of his death. Other hands will also have to finish the valuable *Index to the Botanical Magazine* which he was also compiling.

Mr. Chittenden was elected a Fellow of the Linnean Society in 1908; in 1917 he was awarded the Victoria Medal of Honour by the Royal Horticultural Society and in 1950 he received the O.B.E. for his many services to horticulture. Additional honours paid were the dedication to him of Volume *164* of the *Botanical Magazine* and the award of the Veitch Memorial Medal in 1948.

In 1901 he married Esther Ada Farnes, who survives him. He died on 31 July 1950 at Dedham, where he had been living since his retirement from the Editorship of the Royal Horticultural Society. He was a great horticulturalist, with an unrivalled knowledge of plants and the literature of the subject, an indefatigable and extremely accurate worker who covered a wide field and one whose knowledge and advice were always freely at the service of others; many gardeners and friends are sensible of the great debt they owe him.

VERA HIGGINS.

The passing of the venerable and distinguished botanist, Professor **Boris Alexeievitsch Fedtschenko** leaves a notable gap in the ranks of the older generation of Russian scientists. Fedtschenko was born on the 27 December 1872, and while still at school displayed great interest in natural history, owing to the influence of his mother, who was herself a great traveller and botanist. While a student at Moscow University during the years 1892–1896, Fedtschenko accompanied his mother in botanical excursions to the southern Urals, the Crimea, the Caucasus and Central Asia.

From the year 1897, when Fedtschenko undertook his first independent journey to Turkestan in Central Asia, the vegetation of the Central Asiatic region became the chief object of his studies, which extended over a period of some forty years. His last journey to Central Asia was made in 1934 when he investigated the flora of Tadjikistan.

In 1900 he took up an appointment in the St. Petersburg Botanic Garden (now the Botanical Institute of the Academy of Sciences of the U.S.S.R.). He was at first the Curator of the Turkestan Herbarium and later, in 1905, was promoted to the post of Chief of the Herbarium, a post he held until 1932. During these years he did much to build up the Herbarium and it was greatly enriched with collections made by a number of expeditions to Central Asia, Siberia and the Far East, organized by him.

Fedtschenko was a prolific writer and published many valuable accounts of his botanical studies and particularly of his investigations of the flora of Central Asia. He was the initiator of the Flora of the U.S.S.R. and the first author to contribute to the Flora in 1929. In later years he was one of the most active contributors to this important publication, being responsible for the accounts of the family Berberidaceae and the genera *Megacarpaea*, *Hedysarum*, *Vicia*, *Lens* and *Lathyrus*.

On the occasion of his seventieth anniversary an account of Fedtschenko's life and work by R. J. Rojevitz was published in *Sovetskaya Botanica*, 1940, no. 3, with a list of his works. He was elected a Foreign Member of the Linnean Society in 1936. His death occurred on 29 September 1947, at Leningrad.

The writer is indebted for the material in this notice to Professor A. A. Fedorov, Acting Director of the V. L. Komarov Botanical Institute of the Academy of Sciences of the U.S.S.R. H. S. MARSHALL.

William Inder. All Bob Inder's friends, and they were many, will have read with sorrow and regret of his death early in 1950. He was elected a Fellow of the Linnean Society in 1932.

He was a keen botanist and an excellent forester, but he was also a man of wide interests—well read in all that interested him. This, added to a lively wit, made him an excellent talker and a most pleasant companion.

His character was marked by a very sturdy independence which made him at times, perhaps, too impatient of red tape and the regular official channel. These feelings were probably strengthened by the happy years he spent as D.F.O. in the Surat Dangs where he was in addition the Political Agent for the local Bhil rajahs or headmen: a position in which his hands were reasonably free.

He went up to Oxford in 1909 to take his Forest Diploma, but before this he had already taken his degree at Cambridge and for a short time tried his hand at school mastering, a career he was unlikely to find satisfying—and he did not.

He was posted to Bombay in 1911 and spent nearly all his service in the Northern Circle of the Presidency, though a brief visit to Sind late in his service was unfortunately not long enough to enable him to complete his Sind Flora.

He retired in 1937 and after returning to India for a short tour in 1939, to write a report on the Baroda forests for that State, settled down to retirement

in North Wales. There he was very fully occupied with various local activities during the war.

Bob Inder had been seriously ill for many months, happily ignorant of the hopelessness of his case. He will be sadly missed by all who knew him.

D. B. SOTHERS.

Henry John Jeffery, elected a Fellow in 1909, died at Peacehaven, Sussex, on 24 July 1950, aged sixty-five. Born and educated in London, he received a training in horticulture at the School of Gardening of the Royal Botanic Society, Regent's Park, but, studying at Birkbeck College, in 1904 he was awarded a National Scholarship in Geology and proceeded to the Royal College of Science, South Kensington. Here he decided to devote himself to biological studies and obtained a first class Associateship (A.R.C.S.) in botany in 1907. In the latter year Jeffery was appointed Lecturer in Botany at the School of Pharmacy of the Pharmaceutical Society at Bloomsbury, where he remained until 1911, lecturing during the same period also to the botanical classes at the South-Western Polytechnic, Chelsea. It thus seemed likely that Jeffery's future lay as a teacher, a career for which his painstaking and careful work would have well fitted him; but in 1911 he accepted a post at the Imperial Institute, South Kensington, where, as Special Assistant to Dr. T. A. Henry, then Superintendent of Laboratories, his chief duties were in connection with the preparation of the Bulletin of the Imperial Institute and of the increasing number of official publications of the Institute. Subsequently he assumed charge of the Library and mastered its resources, an experience which stood him in good stead when, in 1926, he was transferred to the Intelligence Section of the Plant and Animal Products Department on the reorganization of the Institute. Jeffery was particularly well suited to his new office. His industry and success in tracing and assessing the worth of information on difficult subjects were most valuable both to colleagues and inquirers, and were much appreciated not least by personal callers at the Institute who recognized his readiness to help them in solving their problems, while his friendly assistance endeared him to his fellow-workers, many of whom were aware of his sympathetic character. In 1936 he succeeded to the vice-principalship of his department.

Work on the Bulletin occupied much of Jeffery's time throughout his service of thirty-three years. He became sub-editor and, later, general editor of the Journal, preparing for publication the reports on investigations carried out in the laboratories of the Institute and compiling technical articles. Apart from his official duties Jeffery was joint author, with the late J. F. Bevis, of *British Plants: their Biology and Ecology* (1911), issued in a revised and enlarged edition in 1920. He was a member of the London Natural History Society and of the Geologists' Association.

Jeffery married Miss Georgina C. Lewis in 1912; she died in 1942. On his retirement in 1944 he removed from London to Peacehaven where he took up, with much interest, the study of British Coleoptera; latterly he had found time to assist in organizing the activities of the local football club and sports association. He is survived by his only son. S. E. CHANDLER.

SIR **Murdoch Campbell McLeod,** second Baronet, was born in Calcutta on 17 July 1893, and succeeded to the title in 1936. He was educated at Winchester and served in the Seaforth Highlanders, 1914–18, on the general staff; he married in 1920. He formed a large collection of Lepidoptera from Assam and Burma which he presented to the Hope Department, Oxford University Museum. He was elected a Fellow of the Linnean Society in 1943. His death occurred in 1950. G. D. HALE CARPENTER.

Many will regret and even mourn the passing of Miss **Emilia Frances Noel,** who died on 19 March 1950. She had been a Fellow of the Society since 1905 and was among the twenty or so senior women-members. Everyone will miss her once regular attendance at the Meetings, where in later years she usually sat in the front row because of failing eyesight.

Perhaps her most distinguishing qualities were her great love for travel and scientific investigation both at home and abroad, and the originality and independence of her character. This latter was manifest at the Swanley Horticultural College in the early part of the century, when she was an advanced and senior student living in private rooms, and the writer was an immature first year in a small new boarding house. Her housemates thought it no small honour when on one occasion Miss Noel and her friend Miss Morrell took her under their wing to a village magic lantern show. Miss Noel gained prizes in her second year for the best diary of garden work and the best notebook of advanced botany. Before her Swanley years she was at Somerville College, Oxford.

Her foreign travels had already begun in 1892 with a visit to Egypt, followed after her college career by a journey to India including Kashmir; and they ended about 1938 with a trip to the Canaries and West Africa. In between she travelled much in Europe, going to France, Spain, Italy, Germany, Sweden and Norway, Corsica, Sicily, Czechoslovakia, Poland and Denmark; farther afield to the Caucasus, Malta, Morocco, Cyprus and Palestine; and farther still to the West Indies, British Guiana, Canada and the United States, South Africa, Ceylon, Australia, New Zealand, Java and Lombok.

She noticed and remembered an amazing amount. The writer once invited her to name the origin of a little bit of embroidery from somewhere in Europe, and after a moment of thought she said somewhere near Marseilles. It was actually purchased in Toulon.

In the first world war she registered for Women's War Service, and during and between both wars she travelled a great deal in England. Her field diary begun in 1919 contains names of a very large proportion of the plants of the British Flora.

Miss Noel was deeply attached to her family homes in Rutland and Lincolnshire. She was the third daughter and youngest child of the Hon. Henry Lewis Noel, a son of the first Earl of Gainsborough; and a first cousin of the third Earl, who collaborated with Mr. A. R. Horwood, latterly of Kew, in the *Flora of Rutland and Northamptonshire*.

During her travels she made many diary note books with sketches, the more important of which are bequeathed to the Royal Geographical Society, and during her life she made many gifts to libraries and museums. She published a small book in 1905 with a list of plants she found in Kashmir and some interesting notes on the country. She published also, some years later, a volume of historical letters and sketches belonging to her family, many dating from the 18th century. This was well reviewed in the London papers as throwing most interesting sidelights on the fashions and happenings of those times.

M. Muriel Whiting.

John Brooke Scrivenor, I.S.O., M.A., F.G.S., for many years Director of the Geological Survey of the Federated Malay States, was the younger son of the Rev. Arthur Scrivenor. He was born at Horncastle, Lincolnshire, 7 December 1876, was educated at King's School, Canterbury, and Hertford College, Oxford, where he studied geology under W. J. Sollas and Herbert H. Thomas, then assistant to the professor.

In the latter part of 1900 he journeyed to Patagonia. In 1902 he joined the Geological Survey of Great Britain, and in 1903 went to the Malay States as first Government geologist. At first he worked quite alone in a country in

which funds were short, transport difficult, and rock exposures extremely poor. Many of his lonely journeys were, he has said, ' the reverse of pleasant owing to the constant dampness, leeches, and the unwelcome proximity of tigers . . .'

He published many papers and reports on the geology of Malaya which he summarized in a book on the geology in 1931 and in an earlier work, *The Geology of Malayan Ore-deposits* (1928).

He retired in 1931, but was actively engaged on geological problems right up to the date of his sudden death at his home at Bedford on 21 April 1950.

One of the problems to which Scrivenor devoted much attention after his retirement was the nature of certain siliceous bodies believed to be sponge-spicules, found in a rhyolite-ash at about 150 feet above sea-level and described in a paper in the Geological Magazine in 1930. They were then referred to as ' marine sponges ', the implication being that the sea stood in geologically recent times at this high level. Further examination, however, threw doubt on this identification. Scrivenor made a study of fresh-water sponges, and concluded that there was no evidence of marine organisms in the ash, and therefore the siliceous bodies provided no evidence of a former sea-level about 150 feet higher than now in Malaya. He published his results in 1943 and 1946, and was careful to state his conclusions clearly in two papers. One of these was read before the Linnean Society on 11 April 1942 as an introduction to a discussion on the biogeographical division of the Indo-Australian archipelago ; the other on the geological and geographical evidence for changes in sea-level in Malaya in historic and pre-historic times, written in 1948, was published in the Journal of the Malayan Branch of the Royal Asiatic Society (1949, *22*, pt. 1, pp. 107–115).

Scrivenor's geological work was interrupted by the 1914–18 war. He served in the Volunteers in Malaya, later coming home to join the Inns of Court O.T.C. (1916–17), and, receiving a commission in the Royal Engineers (Signals), served as Signal Officer to the 171st Infantry Brigade in France in 1918. He published his war-time experience in a small book, *Brigade Signals*.

He married in 1907 Violet, daughter of A. W. Vaisey of Tring and had two sons and a daughter. He was elected a Fellow of the Linnean Society in 1945.

W. Campbell Smith.

Mr. **Harold Walkden** (1885–1949), died at his residence, The Raft, Derbyshire Road, Sale, Manchester, on Good Friday, 15th April, 1949, aged sixty-four years. He was elected a Fellow of the Linnean Society in 1939.

At the age of ten Walken had a severe illness which left a legacy of ill health and interfered with his further attendance at school, but not with his education, for he read widely, and occupied himself in a quiet way with gardening and photography. He became expert in producing still-life photographs of the flowers of hardy plants and of orchids, and a number of these appeared in the Manchester Guardian and other journals.

Walkden's interest in gardening led him to wish to study botany, and in 1915, at the age of thirty, he entered Manchester University as a student under Professor F. E. Weiss, and followed the Honours course in the Department of Botany. In his delicate state of health he was unable to take a Degree, but he attained a high standard of achievement and continued with research. For a number of years (1920 to 1931) he was an Elected Research Student. He had become interested in crown gall on his chrysanthemums, and it was in the Cryptogamic Research Laboratory, under Professor W. H. Lang, and with the active interest of the late Professor Wilfrid Robinson, that Walkden succeeded in isolating from crown gall an organism which was identified as *Bacterium tumefasciens*, Smith and Townsend. An account of this work is published under the title *The isolation of the organism causing crown gall on Chrysanthemum*

frutescens, *L. in Britain* in Annals of Botany, *35*, No. 137, Jan. 1921. He continued and, in collaboration with Robinson, published another paper entitled *A critical study of crown gall* in Annals of Botany, *37*, No. 145, April, 1923. Walkden's nursery garden at Sale provided other problems for investigation, such as fungi causing plant diseases, and the mycorrhizal fungi of orchids (his sister being an expert orchid grower) but his shyness made him reluctant to publish his results.

In his garden he carried out hybridization experiments, chiefly on *Azalea* (*mollis* type), *Delphinium* and *Dianthus*. In the late 1920's he set about trying to improve golden rod (*Solidago Virgaurea*, L.) and grew thousands of plants. After a long struggle he succeeded in producing strains which, after trial at Wisley, gained the Award of Merit of the Royal Horticultural Society. He was interested in local horticultural activities and supported the Sale Horticulture and Allotment Society, of which his cousin, Mr. N. Brownhill, is now President.

Between 1935 and 1947 Mr. Walkden made a series of gifts to the Department of Botany, which began with the presentation of complete sets of Annals of Botany and of The New Phytologist, following this with a gift of money for the purchase of subsequent issues. In 1937, he gave the sum of £100 as 'the nucleus of a fund to assist members of the staff of the Department of Botany in the publication of the results of their researches, primarily with grants in aid of additional plates'. Between that date and 1945 Walkden made further various gifts amounting to £250 to the Walkden Publications Fund, which has proved of great value to the Department. His practical interest in horticulture led him to make, between 1941 and 1947, a further series of gifts amounting to £600, in support of horticultural activities in the Department. Since his death, his sister has informed me that it was his wish that the Department should receive his set of the Journal of Genetics, and other botanical literature.

To his sister, Miss Annice Walkden, his cousin, Mr. N. Brownhill, Professor W. H. Lang, F.R.S., and to the Assistant Registrar of the University, Mr. F. P. Walton, I am indebted for much of the above information, and am glad of this opportunity of placing it on record. To his colleagues in the Department he was an attractive personality, obviously in delicate health, yet uncomplaining and reticent. He was interested in his work for its own sake, and patiently bore with his limitations. Moreover, he had a great fund of practical sympathy for others. He is survived by three sisters. W. O. HOWARTH.

Alfred James Wilmott, who died suddenly on 26 January 1950, was for many years one of the best known figures among students of British and European flowering plants. The son of Alfred John Wilmott, he was born at Tottenham on 31 December 1888, but his father soon after was appointed lecturer in history and classics at Homerton Training College, and at Cambridge the boy was brought up. He was educated at the Cambridge County School, where he studied botany under Dr. Maria Dawson, and at St. John's College, where he had won a scholarship in 1906. He took firsts in both parts of the Natural Sciences Tripos, won a Hutchinson Scholarship at St. John's, and was awarded the Frank Smart Prize. While studying physiology under F. F. Blackman, Wilmott devised an improved method of estimating the evolution of oxygen from water-plants during photo-synthesis, and this later formed the subject of a paper, *Assimilation by Submerged Plants in dilute solutions of bicarbonates and of acids : an improved bubble-counting technique*, which was published by the Royal Society in 1921.

At Cambridge Wilmott came under the influence of C. E. Moss, who had become Curator of the University Herbarium in 1908, and Moss suggested to him that he should be a candidate for a vacancy in the Department of Botany, British Museum (Natural History). He obtained the post, which he took up in 1911. In the same year he was elected a Fellow of the Linnean

Society. The European herbarium was then just beginning, and the whole of Wilmott's museum career was devoted to the building up and arrangement of the collections of British and European flowering plants. The task is, of its very nature, yet unfinished, but, broadly speaking, the British and European Herbarium at South Kensington, as it exists to-day, is Wilmott's creation. He was promoted Deputy Keeper in 1931.

Soon after his appointment to the Museum, Wilmott began to contribute papers and notes of varying length to the Journal of Botany. The earliest of these was *On the name Viola canina*, published in September 1911, and from then until January 1942 his contributions to the Journal were frequent. Among the more notable of them were :—*Oxalis corniculata Linn.*, June 1915 ; *What is Viola montana L.?*, September 1916 ; *British Pulmonarias*, September 1917 ; *The Red Currant*, January 1918 ; *Two new plants from Macedonia*, May 1918, in which he described new species of *Paliurus* and *Calamintha* from specimens collected by Dr. John Ramsbottom while on military service ; *Geranium purpureum, T. F. Forster*, April 1921 ; *Two Alchemillas New to Britain*, June 1922 ; *Myosotis sicula Gussone in Jersey*, August 1923, in which he described a discovery on one of the earlier of the many botanical tours he made with the late Francis Druce ; *The Irish 'Spiranthes Romanzoffiana'*, May 1927, one of Wilmott's most notable papers, again the result of a journey taken with Francis Druce, in which he separates the Irish plants into two species, the southern *S. gemmipara* and the northern *S. stricta* ; *Annotationes Systematicae* I, May 1929, the first of nine papers, appearing at intervals from this date up to January 1942, in which Wilmott, *inter alia*, described some new species from Spain ; *An addition to the Breckland Flora : Veronica praecox All.*, June 1933 ; *Notes on a short visit to Barra*, July 1939 ; and *Some British Species of Rhinanthus*, September 1940, an important paper on a genus to which Wilmott paid special attention. After the death of George Claridge Druce, the Botanical Society and Exchange Club (now the Botanical Society of the British Isles) entered upon a new phase of its history, and in this Wilmott played a leading part, editing many of its publications and contributing to them articles and notes of various kinds.

A reference to the botanical tours of the British Isles, in which Wilmott collaborated with his friend Francis Druce, has already been made. In the course of them most of the classic localities, besides many others previously little known, were visited, with the result that knowledge of the distribution of British plants, and of the present status of the rarer species, was greatly increased. He also collected in Spain, which he visited in 1927 with C. C. Lacaita, and in November of that year he published a short account of the expedition in the Journal of Botany. To one observer, at least, Wilmott's strength seemed to lie in his combination of exceptionally wide knowledge in the field and in the herbarium.

Wilmott's subtle and logical mind was greatly attracted to the study of systematics and of such more difficult genera as *Sorbus* (particularly the whitebeam trees), *Orchis* (particularly the bog orchises), *Rhinanthus*, *Atriplex* (of which he wrote the account for the unfinished Cambridge Flora which Moss edited), *Alchemilla* and *Salicornia*. To the last-named he gave a very great deal of time in his last years, and seemed, so far as it was possible for friends to judge from hearing him talk upon the subject, to be achieving, perhaps for the first time, a real understanding of the forms growing on the British coast. It was a great disappointment that he never completed any written account of them.

It became obvious, however, that Wilmott, in spite of the number of his scattered papers and notes, was one of those who find it very hard to bridge the gap between study and the considered setting down of its results in book form. Partly this was due to the character of his official post, which laid him open

to continual interruption—and here it should be said that no one was kinder to enquirers, or took more trouble to help them with any problems arising from the British or European floras than he. But partly also it was temperamental, and as a result he never wrote either extensive specialized treatises on individual groups, or, more particularly, the new flora of Britain which his friends always hoped he would compile. In the end, though he wrote some fairly long papers, such as that *Concerning the History of the British Flora*, published in Paris by the Société de Biogéographie in 1930, and the lecture on *Systematic Botany from Linnaeus to Darwin*, given in the rooms of the Linnean Society on 26 January 1949, he had no book to his credit, with the exception of the 10th edition, 1922, of C. C. Babington's *Manual of British Botany*, which he edited and to which he contributed a useful appendix containing some of the more important of the recently recognized species and varieties. His paper on *A New Method for the Identification and Study of Critical Groups*, read in title before this Society on 9 March 1950, is still in process of publication as I write.

Wilmott was a man of big frame. In his young days he had been a good athlete, particularly as a player of Association football, a game to which he owed a knee injury which troubled him on and off to the end of his life. Afterwards he became a skilful devotee of table tennis, playing in international matches and thrice winning the British veterans' championship. He had some skill both on the piano and the violin. It was characteristic of him that, in spite of a known cardiac weakness, he was actively engaged, both in his work and his recreations, almost up to the moment of his sudden death. He had played table tennis and delivered a students' lecture on *Geographical Distribution and Classification* within a day or so of his end.

It is not for an amateur to pass judgment on A. J. Wilmott's position as a botanist; all that is permissible is to say something of his character and of his gift of stimulating the botanical interest and enthusiasm of others. In spite of his robust appearance, he was a man of highly strung nervous temperament, which led to the sudden indignant outbursts—intellectual not personal, in their occasion—which would at times interrupt the habitual friendliness of his manner. In the herbarium it was never too much trouble for him to help a visitor with an identification and, if he thought the visitor was on the track of something interesting, to encourage him to follow it up and, if necessary, publish the results. On a botanical expedition he was an admirable companion and leader, tirelessly energetic, with a very quick and sure eye and a gift of commentary which sprang from wide knowledge and was always to the point. Among British botanists, whether professional or amateur, he was both a character and a fertile source of ideas. His burly figure, with rolling gait and capacious white vasculum slung from his shoulder, will be greatly missed.

In 1914, A. J. Wilmott married Miss Jessie Bell, who survives him with one son.

Iolo A. Williams.

Richard Woltereck, F.M.L.S., was born in Hanover in 1877 and spent his boyhood there. He went to the University at Freiburg to study medicine, but he did not pursue these studies very far as he came under the influence of Weismann and turned over to zoology. He graduated in 1898 with a dissertation on the maturation and cleavage of Ostracod eggs. He then left Freiburg and went to the University at Leipzig preparatory to joining Chun on the Valdivia Tief-See Expedition. He started out on this expedition but had to return when they got as far as West Africa owing to a severe attack of malaria. His interest in marine zoology had, however, been aroused and he started some excellent work on the embryology of the Archiannelid *Polygordius* and followed this with some faunistic works on some of the

Coelenterata and Crustacea brought back by the Valdivia Expedition. He became friendly with a young zoologist, Hans Kupelwieser, who was studying in Leipzig and whose father, a wealthy Austrian industrialist, took great interest in science and had built a laboratory on the lake at Lunz in order that his son might study hydrobiology there. Hans Kupelwieser, however, went to continue his studies in California, and his father turned to young Woltereck and asked him if he would undertake the organization and direction of the new station. This Woltereck did with characteristic enthusiasm and energy and by 1905 he had collected a team of scientists, together competent to deal with the zoological, botanical, and chemical aspects of limnology.

The post-glacial lakes of Europe and North America are particularly suitable for the study of the evolution of races. Coregonid fishes, pulmonate mollusca and the crustacean genera *Daphnia* and *Bosmina* have all evolved into numerous closely related races, most of which have become differentiated in the last ten to twenty thousand years. The development of such races must have been brought about by such factors as isolation, natural selection and directed or undirected factors of a changing environment. It was towards an understanding of these factors that Woltereck directed the researches at Lunz. At first the main consideration was the evolution of the fishes, and several tanks were built with arrangements for thermostatic control; but this work was not carried very far as Woltereck started work on *Daphnia* and other Cladocera and found that they were particularly suitable for studies of the kind he had in mind. It was unravelling the complex taxonomic problems of *Daphnia* and the relationships of different forms to the environment and their evolution that occupied him for the rest of his life. There were many visitors at this time to Lunz from all parts of the world including Mr. D. J. Scourfield, F.L.S. The organization impressed these visitors very much and Scourfield returned to this country to urge the setting up of a freshwater biological station over here.

In 1908 Woltereck brought out the first number of the Internationale Revue der gesamten Hydrobiologie und Hydrographie. He continued to edit this important scientific journal until it was brought to a halt in 1943 by the effects of the war. By this time over forty volumes had appeared with articles on all aspects of hydrobiology by scientists from all parts of the world. It is gratifying to learn that the journal is to be started again shortly under the editorship of his daughter, Dr. Eva Roth-Woltereck, assisted by ten sub-editors from many countries, including Great Britain.

Hans Kupelwieser took over the running of the station at Lunz at about this time, and Woltereck continued his studies on *Daphnia* at Leipzig until the outbreak of the war in 1914 when he had to give up scientific work and went first to Rome and later to Bern where he was concerned with the care of prisoners of war. After the war he continued with relief measures in Rome and Sofia until 1926 when he had an accident and was laid up for a year. During all this time, although he was unable to continue his scientific experiments, he still kept his eyes on *Daphnia*, and in 1922 discovered that a race was established in lake Nemi which agreed in its details with a race he had transported in 1913 in large numbers as resting eggs from a lake in Denmark to this and other Italian lakes. Many previous attempts had been made to find descendants but these had all been unsuccessful; from now on however the *Daphnia* multiplied rapidly and it seemed that a new hereditary race fitted for the lake Nemi environment had been established. Woltereck was very much stimulated by this result and set up a new station at Seeon in the Chiemgau in the midst of a large number of small lakes suitable for his studies on mass populations of *Daphnia*. His work on these lakes threw light on many problems and he was able to relate the shape and other peculiarities of the various races to the nature of the water in which they were living. This he was able to confirm very

strikingly when, in 1931, he continued this type of work in the North American lakes. He found that in European lakes most of the forms of pelagic *Daphnia* are derivatives of *Daphnia longispina*, but that in North America they belong to the *D. pulex* series. In both series similar changes of forms are found as the habitat alters from a littoral to a more pelagic type. He found that every lake has stratified water in the summer and that at that time the different populations or races of *Daphnia* are also stratified; some belonging above the thermocline, some below it and some very near it. Very often he was able to show morphological differences between these populations, and he produced considerable evidence that the shape of the tall helmet that is found in several races of *Daphnia* at certain times of the year is related to the direction of swimming, and is one of the factors keeping the population of *Daphnia* at its particular level in the lake. He considered that the close correlation between the condition of life and the morphological characters of the races proved that the evolution of the different races of *Daphnia* was caused or at least directed by environmental factors. The successful outcome of Woltereck's researches was due to the efficient and energetic way in which he integrated widely different studies, by combining careful taxonomy with accurately recorded field work and following these with well-planned experimental studies in the lakes as well as in the laboratory. His work on the effect of isolation and endemism on races of *Daphnia* led him to consider these problems in a broader aspect and his American tour was preparatory to a world wide one, particularly in the Pacific Islands. After lecturing in many of the American Universities he visited Hawaii, the Philippines and Japan, and spent some time in the East Indies leading the Wallacea Expedition. In 1933, at the invitation of the Turkish Government, he became professor of zoology at the Agricultural College at Ankara. He was attracted to this post by the fact that there are a great many lakes in Anatolia which had never been explored in a biological sense. He spent much of his time investigating those lakes and concerned himself with inland fishery problems. He was on leave in Germany when war broke out in 1939 and did not return to Turkey. In 1942 he was collecting in Capri when he had a fall in a stream and hurt his back. At first it was not thought that his injury was particularly serious but he remained an invalid until the spring of 1944 when he died at his home at Seeon.

He married Margarete Hoffmann in 1900 and had a son and two daughters.

J. P. HARDING.

ADDITIONS AND DONATIONS TO THE LIBRARY 1949–50

Note.—Names of donors are given in square brackets. Separate copies of papers which are included in periodicals received by the Library are no longer catalogued.

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——. The world was my garden. Pp. xiv+494. 8vo. *New York*, 1948. [Author.]

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BENEFACTIONS

LIST *in accordance with Bye-Laws, Chap.* 17, *Sect.* 1. *of all Donations of the amount or value of Twenty pounds and upwards, received during the past five years.*

1946

The Royal Society : Grant-in-aid of publications, £800.

1947

The Royal Society : Grant-in-aid of publications, £750.
Anonymous Donor : Towards the reorganization of the Library, £100 ; and two mahogany bookshelves.
Mr. Reginald L. Hine, F.S.A. : Manuscript botanical note-book written by Thomas Lawson in 1676–77.

1948

The Royal Society : Grant-in-aid of publications, £750.
Dr. J. Jaramillo-Arango : Donation towards cost of plates for his paper in *Journal, Botany*, £45.
The Pilgrim Trust : Grant to form the nucleus of the Library Restoration Fund, £2500.
Royal Academy, Inverness : Copy of Thornton's *A new illustration of the Sexual System of Linnaeus*.
Imperial Chemical Industries : Donation to the Library Restoration Fund, £50.
Royal Horticultural Society : Donation to the Library Restoration Fund, £105.
Zoological Society of London : Donation to the Library Restoration Fund, £25.
Dr. G. H. Pethybridge : Bequest for general purposes, £100.

1949

The Royal Society : Grant-in-aid of publications, £750 ; Grant-in-aid of the Library, £250.
Mrs. C. M. Snow, F.L.S. : Donation to the Library Restoration Fund, £30.
Colonel F. C. Stern, O.B.E., M.C. : Donation to the Library Restoration Fund, £45.
Mr. A. E. Günther : 42 volumes of the late Dr. Albert Günther's work books , with a book-case.
Imperial Botanical Conference Trustees : Donation to the Library Restoration Fund, £57 4*s*. 11*d*.
Anonymous donor : £25 to the Library Restoration Fund.
The late Mr. R. J. Flintoff, F.L.S. : £1000 free of Legacy Duty.
Research Committee of the University of Liverpool : Donation towards the cost of Dr. C. Leighton Hare's paper on *Eriocaulon*, £25.
Miss I. M. Hayward : Bequest of £100 for general purposes.
Mr. D. J. Scourfield, I.S.O. : Bequest of £100 for general purposes.

1950

The Royal Society : Grant-in-aid of publications, £750.
Miss E. F. Noel : Bequest of £100 for general purposes.
Mr. E. A. Robins : Long run of the Society's publications.
Mr. W. C. Barton : Long run of the Society's publications.
Mrs. E. W. Sexton : Donation towards the cost of the joint paper on *Jassa* in the *Journal, Zoology*, £50.

General

1948–49 £	RECEIPTS	£ s. d.	1949–50 £ s. d.
	To Balance at 1 May 1949 :—		
	Current Account at Bank	17 6 10	
	Deposit Account Post Office Savings Bank	525 19 0	
	Cash in hand	14 15 9	
	Awaiting Investment	55 2 9	
581			613 4 4
248	,, Admission Fees		164 0 0
	,, Arrears of Annual Contributions	64 13 0	
	,, Annual Contributions for year	2613 7 8	
	Do. in advance	59 2 4	
2613			2737 3 0
16	,, Do. of Associates		27 6 0
262	,, Composition Fees		280 10 0
328	,, Interest on Investments (including Income Tax recovered)		334 12 4
114	,, Do. Post Office Savings Bank Account		116 16 6
	,, Sales of Publications :—		
	Transactions	33 13 8	
	Journals	488 5 10	
	Proceedings &c.	195 12 1	
762			717 11 7
750	,, Grants in aid of Publications		775 0 0
20	,, Miscellaneous Receipts		73 16 6
1000	,, Transfer from Reserve for Publications Fund		56 18 1
45	,, Donation.—Dr. Jaramillo-Arango		....
100	,, Bequest.—Dr. G. H. Pethybridge		....
—	,, ,, Miss I. M. Hayward		100 0 0
—	,, ,, D. J. Scourfield		100 0 0
—	,, War Damage Account		9 0 0
£6839			£6105 18 4

Library

£		£ s. d
127	To Balance at 1 May 1949	294 13 5
45	,, Interest on Investments (including Income Tax recovered)	55 8 5
11	,, Donation : Imperial Chemical Industries	10 10 0
300	,, Transfer from General Account	250 0 0
2	,, Miscellaneous Receipts	8 6
—	,, Bequest.—R. J. Flintoff	1000 0 0
£485		£1611 0 4

Library

£		£ s. d.
2615	To Balance at 1 May 1949 :—	1884 5 5
105	,, Donations : Royal Horticultural Society	....
50	Imperial Chemical Industries	....
25	The Zoological Society	....
19	Fellows and Friends	53 17 0
—	The Royal Society	250 0 0
—	The Trustees, Imperial Botanical Conference 1935.	57 4 11
£2993		£2245 7 4

Fellows' Postal

		£ s. d.
50	To Balance at 1 May 1949	50 6 5

Account

1948–49 £	PAYMENTS	£ s. d.	1949–50 £ s. d.
199	By Coal, Electric Current, and Gas		196 3 1
45	,, Repairs : Sundry		49 7 1
86	,, Taxes and Insurance		91 17 1
305	,, Miscellaneous Printing and Stationery		222 17 11
265	,, Petty Expenses and Postages		270 3 6
	,, Publications :—		
	Printing	1287 14 5	
	Distribution	78 6 2	
	Illustrations	125 17 6	
2126			1491 18 1
900	,, Transfer to Reserve for Publications Fund		700 0 0
1617	,, Salaries and Wages		1580 0 0
15	,, 'Zoological Record' (Vol. 85) Donation		15 0 0
5	,, The Biological Council—Donation		....
—	,, International Union for Nature Protection—Donation		27 2 0
100	,, Staff Annuities (Annual Premiums)		100 0 0
259	,, Purchase of £326 8*s.* 7*d.* 2½ per cent. Consolidated Stock (Compounders' Fees)		....
—	,, Purchase of £496 18*s.* 4*d.* 2½ per cent. Consolidated Stock (Compounders' Fees)		368 2 9
4	,, Linnean Medals		14 4 7
300	,, Transfer to Library Account		250 0 0
	,, Balance at 30 April 1950 :—		
	Current Account at Bank	702 10 10	
	Deposit Account Post Office Savings Bank	—	
	Cash in hand	6 11 5	
	Amount awaiting Investment	20 0 0	
613			729 2 3
£6839			£6105 18 4

Account

£		£ s. d.	£ s. d
149	By Periodicals		289 4 6
12	,, Binding		157 2 0
29	,, Books		32 8 1
—	,, Purchase of £1414 7*s.* 11*d.* 2½ per cent. Consolidated Stock (Flintoff Bequest)		1000 0 0
—	,, Miscellaneous		5 8
	,, Balance at 30 April 1950 :—		
	Current Account	32 0 1	
	Deposit Account Post Office Savings Bank	100 0 0	
295			132 0 1
£485			£1611 0 4

Restoration Fund

£		£ s. d.	£ s. d.
458	By Steel Shelving		....
90	,, Glazing Bookshelves		....
66	,, Alterations (Library Annexe)		....
42	,, Purchase of Foreign Works		2 17 0
437	,, Binding and Repairs to Books		529 11 6
16	,, Miscellaneous		....
	,, Balance at 30 April 1950 :—		
	Current Account at Bank	141 8 10	
	Deposit Account at Bank	571 10 0	
	Deposit Account Post Office Savings Bank	1000 0 0	
1884			1712 18 10
£2993			£2245 7 4

Account

£		£ s. d.
50	By Balance at 30 April 1950	50 6 5

Special Accounts
(Trust and Reserve Funds)

RECEIPTS	£	s.	d.	£	s.	d.
To Balance at 1 May 1949 :—						
Westwood Fund	103	15	10			
Trail Award Fund	15	6	8			
Crisp Award Fund	93	10	2			
Hooker Lecture Fund	135	11	2			
Goodenough Fund		8	0			
Minchin Fellowship Fund	4	10	5			
Carnegie Corporation Grant	419	3	7			
Reserve Fund	431	1	2			
Reserve for Publications Fund	1903	10	0			
Deposit (Dr. A. H. Uggla)	15	0	0			
				3121	17	0
,, Transfer from General Account :—						
Reserve for Publications Fund		....		700	0	0
,, Interest on Investments (including Income Tax recovered) :—						
Westwood Fund	10	17	4			
Trail Award Fund	3	10	0			
Crisp Award Fund	10	5	0			
Hooker Lecture Fund	21	18	0			
Goodenough Fund	8	12	8			
Minchin Fellowship Fund	3	0	0			
Staff Pension Fund	8	7	8			
				66	10	8
				£3888	7	8

PAYMENTS	£	s.	d.	£	s.	d.
By Reserve for Publications Fund :—						
Transfer to General Account		....		56	18	1
,, Staff Pension Fund :—						
Purchase of £8 9s. 8d. 3 per cent. Savings Bonds 1955/65		....		8	7	8
Crisp Award :—						
,, Purchase of £148 1s. 0d. 2½ per cent. Consolidated Stock		....		103	15	2
,, Hooker Lecture, 1948 (cost of Publication)		....		22	2	6
,, Balance at 30 April 1950 :—						
Westwood Fund	114	13	2			
Trail Award Fund	18	16	8			
Crisp Award Fund		....				
Hooker Lecture Fund	135	6	8			
Goodenough Fund	9	0	8			
Minchin Fellowship Fund	7	10	5			
Carnegie Corporation Grant	419	3	7			
Reserve Fund (for balance of cost of Central Heating)	431	1	2			
Reserve for Publications Fund	2546	11	11			
Dr. A. H. Uggla (Deposit)	15	0	0			
				*3697	4	3
				£3888	7	8

* Including £3689 19s. 0d. in Post Office Savings Bank.

Investments on 30 *April* 1950

£	s.	d.	*General Account*		*Market Value 30 April 1950.* £	s.	d.
1000	0	0	3½ per cent. London County Consolidated Stock 1958–68	@ 101½	1015	0	0
1548	8	9	British Transport 3 per cent. Guaranteed Stock 1978–88	@ 89	1378	2	2
338	6	8	3½ per cent. War Stock	@ 91½	309	11	6
1000	0	0	2½ per cent. Defence Bonds	@ 100	1000	0	0
2199	18	6	4 per cent. Australian Stock 1961–64	@ 105½	2320	18	5
200	0	0	3 per cent. War Stock 1955–59	@ 103	206	0	0
1139	13	0	3 per cent. Savings Bonds 1955–65	@ 99½	1133	19	0
2637	5	5	2½ per cent. Consolidated Stock	@ 69	1819	14	4
176	19	3	3 per cent. Savings Bonds 1960–70	@ 96	169	17	8
274	5	5	3 per cent. Treasury Stock	@ 80½	220	15	9
496	18	4	2½ per cent. Consolidated Stock	@ 69	342	17	5
					£9916	16	3

£	s.	d.	*Library Account*		£	s.	d.
471	18	9	British Transport 3 per cent. Guaranteed Stock 1978 88 (Bentham Bequest)	@ 89	420	0	6
103	12	5	Surrey County 3 per cent. Stock 1961–66 (Wakehurst Bequest)	@ 95½	98	19	2
191	12	7	4 per cent. Australian Stock 1961–64 (Walker & Morey Bequests)	@ 105½	202	3	4
107	2	1	2½ per cent. Consolidated Stock (Stebbing Bequest)	@ 69	73	18	0
530	0	0	3 per cent. Savings Bonds 1960–70 (Tagart Bequest)	@ 96	508	16	0
1414	7	11	2½ per cent. Consolidated Stock (Flintoff Bequest)	@ 69	975	18	8
					£2279	15	8

£	s.	d.	*Special Accounts*		£	s.	d.
£1063 10 7	232	5	0	Metropolitan Water Board 3 per cent. " B " Stock (Westwood Bequest)	@ 84½	196	5	1
	667	14	2	Ditto ditto (Hooker Lecture Fund)	@ 84½	564	4	3
	163	11	5	Ditto ditto (Goodenough Fund)	@ 84½	138	4	4
	100	0	0	New South Wales 3½ per cent. Stock 1930–50 (Trail Award Fund)	@ 101½	101	10	0
	409	11	1	2½ per cent. Consolidated Stock (Crisp Award Fund)	@ 69	282	11	10
	148	1	0	,, ,, ,, (Crisp Award Fund)	@ 69	102	3	1
£380 10 6	156	7	2	,, ,, ,, (Westwood Fund)	@ 69	107	17	9
	74	14	6	,, ,, ,, (Hooker Lecture Fund)	@ 69	51	11	3
	149	8	10	,, ,, ,, (Goodenough Fund)	@ 69	103	2	4
	277	9	6	3 per cent. Savings Bonds 1955–65 (Staff Pension Fund)	@ 99½	276	1	9
	8	9	8	,, ,, ,, 1955–65 (Staff Pension Fund)	@ 99½	8	8	9
	100	0	0	,, ,, ,, 1960–70 (Minchin Fund)	@ 96	96	0	0
				F. C. STERN, *Treasurer.*		£2028	0	5

We have (in conjunction with the Professional Auditors, who certify as to all details) audited the Accounts of the Society for the year ended 30 April 1950 and found them correct. We have verified the Investments and Bank Balances.

18th May 1950.

W. B. KEEN & Co., *Chartered Accountants*,
Finsbury Circus House,
Blomfield Street, London, E.C.2.

B. BARNES,
I. H. BURKILL,
A. TINDELL HOPWOOD,
H. W. PARKER.
GEORGE TAYLOR,
E. M. WAKEFIELD,
} *Audit Committee.*

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THE SYSTEMATICS ASSOCIATION

Annual Report VIII (1948–1949)

The Seventh Annual Report covering the years 1947-1948 was adopted at the Annual General Meeting held on 25 May 1948 at the Herbarium, Royal Botanical Gardens, Kew. This report has been accepted for publication in the Proceedings of the Linnean Society.

(2) The Association participated with the Linnean Society in arranging and presenting a series of lectures and demonstrations for university students. Three lectures were devoted to the history of Botanical Taxonomy; three to the history of Zoological Taxonomy. Demonstrations at the Linnean Society and the Natural History Museum have already been held, and the third demonstration of Botanical Taxonomy is arranged for 7 May at the Herbarium, Royal Botanical Gardens, Kew.

(3) A joint discussion with the Linnean Society was held on 10 March in the rooms of the Linnean Society. Dr. W. B. Turrill introduced the subject "Cytology as a Factor in Taxonomy". Dr. S. Muldal followed with the description of the breeding systems in species of Earthworms, linking up the study of chromosome numbers and polyploidy with the mode of reproduction with particular reference to obligatory and facultative parthenogenesis, and Col. F. C. Stern gave an account of the chromosome numbers in flowering plants as an additional basis for Taxonomy. The meeting was well attended and the following took part in the general discussion: Dr. S. C. Harland, F.R.S., Prof. T. G. B. Osborn, Prof. A. D. Peacock, Dr. O. W. Richards, Dr. J. Ramsbottom, O.B.E., Dr. D. H. Valentine, Dr. E. F. Warburg, Mr. A. J. Wilmott, Dr. C. R. Metcalfe, Mr. F. C. Grigg, Mr. L. F. La Cour and Prof. W. H. Pearsall from the chair.

(4) "*Evolution*".

A few members have taken advantage of the concession granted by the Society for the Study of Evolution whereby they receive the journal "Evolution" at a reduced rate. Other members wishing to do the same should inform the Manager, Postal Department, William Dawson and Sons, Cannon House, Macklin Street, London, W.C.2, enclosing a remittance of 25*s*., this being the equivalent of one year's subscription plus agency fees to cover cost of distribution.

(5) The activities of the Association's committees have been maintained.

(a) *Research* (Convener Dr. W. B. Turrill).

About twenty correspondents have written in for advice regarding taking up experiments with plants with a bearing on systematics. All letters were answered and advice given. Three or four workers are likely to take up new researches. Seeds and other material have been provided and information given for starting these new researches. Genera involved are *Poterium*, *Bellis*, *Symphytum* and *Parietaria*.

(b) *Maps and Censuses* (Convener Dr. O. W. Richards).

The Committee held one Meeting on 5 November 1948 but it has also worked by individual consultations and by the circulation of Minutes. It has chiefly been concerned with drafting an introduction to the account of the Vice-county system. Two problems to which a lot of detailed consideration had to be given were how to deal with County boundaries which meander

from one side of a River to the other or leave the river bank for short distances, and how to record more or less amphibious species which are seen at river or lake boundaries of Vice-counties.

In December 1948, Mr. Dandy and Mr. Milne-Redhead met officers of the Ordnance survey and were given quotations for the supply of various quantities of the maps which will be required. Later, they saw the officers of the Ray Society, who will almost certainly publish the work when it is finished. The limiting factor in its completion is, as it always has been, the amount of time that Mr. Dandy can afford to give to the detailed preparation.

Mr. Hewer has made a preliminary examination of the best way to record the extra-British Palearctic distribution of British species.

(c) *Education* (Convener Dr. T. G. Tutin).

The Committee has held only one meeting during the year 1948/49. At that meeting the state of the textbooks which are being prepared, was discussed and it was found that progress had been slower than was hoped, but steady. Steps are being taken to speed up the preparation of these books.

It was agreed to suggest that Taxonomic Methods be the subject for the course of lectures to be arranged jointly by the Systematics Association and the Linnean Society for next Session.

(d) *Taxonomic Principles* (Convener Mr. A. H. G. Alston).

Mr. Wilmott's paper on " Intraspecific categories of variation " which he gave at the Botanical Society's Conference on British Critical Groups is in proof and will be distributed to members of the Committee for discussion.

(e) *Handbooks* (Convener Dr. B. M. Hobby).

A new edition of the key work is ready for press. This has been brought up to date and the treatment of the different groups has been made more uniform. An estimate has been tendered for.

J. P. Harding,
R. Melville,
Hon. Secretaries.

Income and Expenditure for the Year 1948–49

ORDINARY ACCOUNT

Receipts	£	s.	d.
Balance at 30 April 1948	113	2	0
Annual Subscriptions	10	5	0
Royalties on sales of New Systematics (to 31 March 1948)	14	5	7
Sales of New Systematics	1	12	11
Donation		10	0
	£139	15	6

Expenditure	£	s.	d.	£	s.	d.
Rent of meeting rooms					10	0
Stationery and Secretarial expenses				5	12	2
Preparation of Vice-County Maps				1	0	0
Subscriptions to Biological Council (2 years)				2	2	0
Balance at Bank				130	11	4
				£139	15	6
Outstanding liabilities						
Clarendon Press	1	13	0	138	2	6

SPECIAL ACCOUNT

Receipts	£	s.	d.
Balance at 30 April 1948	306	18	8
Life membership subscriptions	10	0	0
Interest to 31 December 1948	7	13	0
	£324	11	8

Expenditure	£	s.	d.
Nil			
Balance at Bank	324	11	8

H. W. Parker, *Hon. Treasurer.*

Audited and found correct:

A. H. G. Alston,
J. D. Macdonald, } *Hon. Auditors.*

5 May 1949.

THE SYSTEMATICS ASSOCIATION

Annual Report IX (1949–1950)

The Eighth Annual Report for the years 1948–1949 was adopted at the Annual General Meeting held on 6 May 1949 in the Herbarium of the Royal Botanic Gardens, Kew, at the invitation of the Director. The formal meeting was preceded by a conversazione during which members inspected the exhibits in the Herbarium arranged for the Demonstration on Botanical 'Taxonomy after Linnaeus'. This formed the final demonstration, on 7 May, of the series of lectures and demonstrations for students held during the 1948–1949 session and organized jointly with the Linnean Society.

The Association co-operated with the Linnean Society in organizing a further series of lectures and demonstrations during the 1949–1950 session on "The Practice of Botanical and Zoological Classification".

26 October 1949.	"Dealing with the Raw Material (Plants)" by Mr. B. L. Burtt, F.L.S.
9 November 1949.	"Dealing with the Raw Material (Animals)" by Prof. Alastair Graham.
23 November 1949.	"Fossils in Classification" by Dr. A. Tindell Hopwood, Sec.L.S.
25 January 1950.	"Geographical Distribution and Classification (Plants)" by Mr. A. J. Wilmott, F.L.S.
8 February 1950.	"Geographical Distribution and Classification (Animals)" by Prof. G. D. Hale Carpenter, M.B.E., F.L.S.
22 February 1950.	"Cytology as a Factor in Classification" by Colonel F. C. Stern, O.B.E., M.C., F.L.S.
8 March 1950.	"The Classification of Animals and Plants". Demonstration in the British Museum (Natural History), Cromwell Road, S.W.7.

The final demonstration of the series on "The Methods of Plant Taxonomy" is to take place in the Herbarium, Royal Botanic Gardens, Kew, on Saturday, 6 May 1950.

A joint discussion with the Royal Geographical Society on the Cartographical Presentation of Biological Distributions took place in the rooms of the Royal Geographical Society on Monday, 6 March at 2.30 p.m. The Symposium was opened by Dr. W. B. Turrill who outlined some distributional problems encountered by botanists and posed a number of queries on which botanists wished to have the guidance of cartographers. Mr. H. R. Hewer, who followed, discussed some of the difficulties of mapping animal distributions covering both land masses and oceans and his attempts at solving them. Mrs. M. A. Anderson then gave a very lucid exposition of map projections and the nature of the distortions produced in each, indicating the best compromise that could be made for various distributions. Dr. E. C. Willatts completed the symposium with a discussion of grid systems and a general discussion followed.

The joint discussion with the Linnean Society took the form of a discussion of the application of biometrics to taxonomic problems and was held in the rooms of the Linnean Society on Thursday, 23 March 1950. Dr. R. Melville opened the discussion, touching upon the use of plant indices for discriminating between species and other groups and indicating some of the applications of cartesian and polar coordinates in plant taxonomic studies. Prof. Duncan

Leitch then read a paper on biometrics and systematics in relation to palaeontology, which was followed by a contribution from Dr. C. B. Williams entitled " A statistical examination of the work of systematists ". This was read, in his absence, by Dr. J. P. Harding. The lengthy discussion which followed evidenced considerable interest in the biometrical approach to taxonomic problems.

Activities of Committees.

(a) *Research.*

Dr. W. B. Turrill has resigned from the convenership and Mr. B. L. Burtt, Royal Botanic Gardens, Kew, is now acting in that capacity. A number of requests for advice on research have been received during the year and universities have been asked for information on subjects of research in their departments with the object of co-ordinating research bearing on taxonomy, and preventing duplication of effort.

(b) *Maps and Censuses* (Convener Dr. O. W. Richards).

Mr. Dandy's account of the vice-county system is not quite finished but arrangements have been made for publication as soon as it is ready.

(c) *Education* (Convener Prof. T. G. Tutin).

No meeting has been held during the year, but some progress has been made in the preparation of the textbooks.

(d) *Taxonomic Principles* (Convener Mr. A. H. G. Alston).

No meeting has been held during the year.

(e) *Handbooks* (Convener Dr. B. M. Hobby).

The new edition of the " Key Works " is awaiting a few further additions before going to the press. Dr. Turk's account of the *Acari* has been completed and has been submitted to two referees, both of whom have given very favourable reports. It is now being made ready for the press.

J. P. Harding,
R. Melville,
Hon. Secretaries.

The Systematic Association: Accounts for the Year 1949–50

ORDINARY ACCOUNT.

(Balance taken on 1 May 1950)

Income

	£	s.	d.
Balance at the Westminster Bank on 30 April 1949	130	11	4
Subscriptions	37	5	0
Sale of ' New Systematics ' (2 copies)	1	13	0
Sale of ' Key Works ' (2 copies)		15	0
Royalties on sale of ' New Systematics ' (for the year ending 31 March 1949—245 copies)	25	14	6
	£195	18	10

Expenditure

	£	s.	d.
Secretarial Expenses (stationery, stamps and duplicating)	2	8	11
Linnean Society (printing and rent of room)	11	2	0
Clarendon Press (4 copies of ' New Systematics ' including 2 outstanding from 1949)	3	6	0
Refund of oversubscription		5	0
Balance at bank on 1 May 1950	178	16	11
	£195	18	10
Outstanding:			
Treasurer's Expenses		11	0
Secretaries' Expenses	4	12	0

SPECIAL ACCOUNT.

(Balance taken on 1 May 1950)

Income

	£	s.	d.
Balance in Post Office Savings Account on 30 April 1949	324	11	8
Life Membership Subscription (1)	5	0	0
Donations (Mr. F. J. Manning and Mr. W. H. E. Rivett)	3	5	0
Interest	8	2	3
	£340	18	11

Expenditure

	£	s.	d.
Nil			
Balance at Bank	340	18	11

E. B. Britton, *Hon. Treasurer.*

Audited and found correct:

Victor S. Summerhayes,
B. L. Burtt, } *Hon. Auditors.*

3 May 1950.

PROCEEDINGS OF

THE LINNEAN SOCIETY OF LONDON

162ND SESSION (1949-50)

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A Catalogue of the Linnaean Herbarium, compiled and annotated by Spencer Savage, F.L.S. London, 1945. (Pp. xvi+226, frontisp., 8 plates and pull-out leaf.) £3 net.

Synopses of the British Fauna :—

No. 1. *Opiliones*. By Theodore H. Savory, M.A., F.Z.S. (New Edition.) 2*s*. net.

No. 2. *Caprellidea*. By R. J. Harrison, B.A., A.L.S. 1*s*. 4*d*. net.

No. 3. *Gammaridae* (*Amphipoda*) ; *with Key to the Families of British Gammaridea*. By D. M. Reid, F.L.S., Department of Biology, Harrow School. 3*s*. 4*d*. net.

No. 4. *Freshwater Bivalves* (*Mollusca*),—(*Corbicula, Sphaerium, Dreissena*). By A. E. Ellis, M.A., F.L.S., Biology Department, Epsom College. 2*s*. 6*d*. net.

No. 5. *Freshwater Bivalves* (*Mollusca*).—*Unionacea*. By A. E. Ellis, M.A. F.L.S., Biology Department, Epsom College. 5*s*. net.

No. 6. *Lumbricidae* (*Annelida*), *with a Key to the common species*. Dr. L. Cernosvitov† and Dr. A. C. Evans, Rothamsted Experimental Station. 2*s*. 6*d*. net.

No. 7. *Talitridae* (*Crustacea, Amphipoda*). By D. M. Reid, F.L.S., Department of Biology, Harrow School. 2*s*. 6*sd*. net.

No. 8. *Slugs* (*Mollusca*) (*Testacellidae, Arionidae, Limacidae*). By H. E. Quick, M.B., B.Sc., F.R.C.P. 1949. 2*s*. 6*d*.

Catalogue of the Printed Books and Pamphlets in the Library of the Linnean Society of London. New Edition, London, 1925. (Pp. 860.) 13*s*. 4*d*. net.

General Index to the first Twenty Volumes of the Journal (*Zoology*) .... London, 1896. (Pp. 437.) 6*s*. 8*d*. net.

General Index to the first Twenty Volumes of the Journal (*Botany*) .... London, 1888. (Pp. 428.) 6*s*. 8*d*. net.

The Darwin-Wallace Celebration held on Thursday, 1st July, 1908, *by The Linnean Society of London*. London, 1908. (Pp. 118.) 3*s*. 4*d*. net.

Catalogue of the Manuscripts in the Library of The Linnean Society of London.—Part 1. *The Smith Papers*. (*The Correspondence and Miscellaneous Papers of Sir James Edward Smith, M.D., F.R.S., first President of the Society*.) By Warren R. Dawson, F.R.S.E. London, 1934. (Pp. 114.) 13*s*. 4*d*. net.

—— Part 2. *Caroli Linnaei Determinationes in hortum siccum Joachimi Burseri. The text of the manuscript in the Linnaean Collections*, edited by Spencer Savage, F.L.S. London, 1937. (Pp. 78.) 13*s*. 4*d*. net.

—— Part 3. *Synopsis of the Annotations by Linnaeus and contemporaries in his Library of Printed Books*. By Spencer Savage, F.L.S. London, 1940. (Pp. 20.) 6*s*. 8*d*. net.

—— Part 4. *Calendar of the Ellis Manuscripts*. (*The Correspondence and Miscellaneous Papers of John Ellis, F.R.S.*) By Spencer Savage, F.L.S., Hon. Memb. Sv. Linné-sällsk. (Pp. vi, 104.) London, 1948. 25*s*. net.

'A Prodromus of the British *Hieracia*.' By the late H. W. Pugsley, B.A., F.L.S., has been published as Vol. 54 (No. 351) of the Society's Journal, Botany, comprising pp. iv, 356, and 17 plates. Copies are available for purchase by non-members, £3.

'Lectures on the Development of Taxonomy delivered in the Rooms of the Linnean Society during the Session 1948-49.' London, 1950 4*s*. net.

NOTICE TO CONTRIBUTORS

Papers must be in double-spaced typescript on one side only of sheets of uniform size; and in such a form that no further corrections or alteration will be necessary in proof. *Papers should be written concisely, and thoroughly revised before submission, so as to reduce the cost of printing and proof-correction.* An author is allowed corrections up to 10*s*. 0*d*. a sheet of 16 pages; but must pay for any corrections in excess of that allowance. The International Rules of Nomenclature should be observed.

References to literature should be carefully verified. In short papers, where the references are few and rarely repeated, and also in lists of synonymy and the like, shortened references may conveniently be given in the text (not in footnotes), but the abbreviations *ibid.* and *loc, cit.* should be avoided except where the full reference is on the same page. In longer papers, where the references are numerous and frequently repeated, the full references should be given in a 'List of Works referred to' at the end of the paper. This should be arranged with the names of the authors in alphabetical order, and with the papers under each author's name in chronological order, the date of publication preceding the title of the paper. Where more than one paper by the same author appears in a single year they should be distinguished by *a, b, c,* . . . Where it is desirable to shorten a long title, omissions should be indicated by three full stops. Titles of books and papers (*which must always be given*) in periodicals should be in italics, and contractions should be those used in standard taxonomic works. The volume number should be in italic Arabic numerals and the plate number (indicated by Pl.) together with the pagination (which should always be given) in Arabic numerals. References in the text to the 'List of Works referred to' should be made by the name of the author and the year of publication. Except in headings, scientific names up to generic rank should be marked for italics.

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